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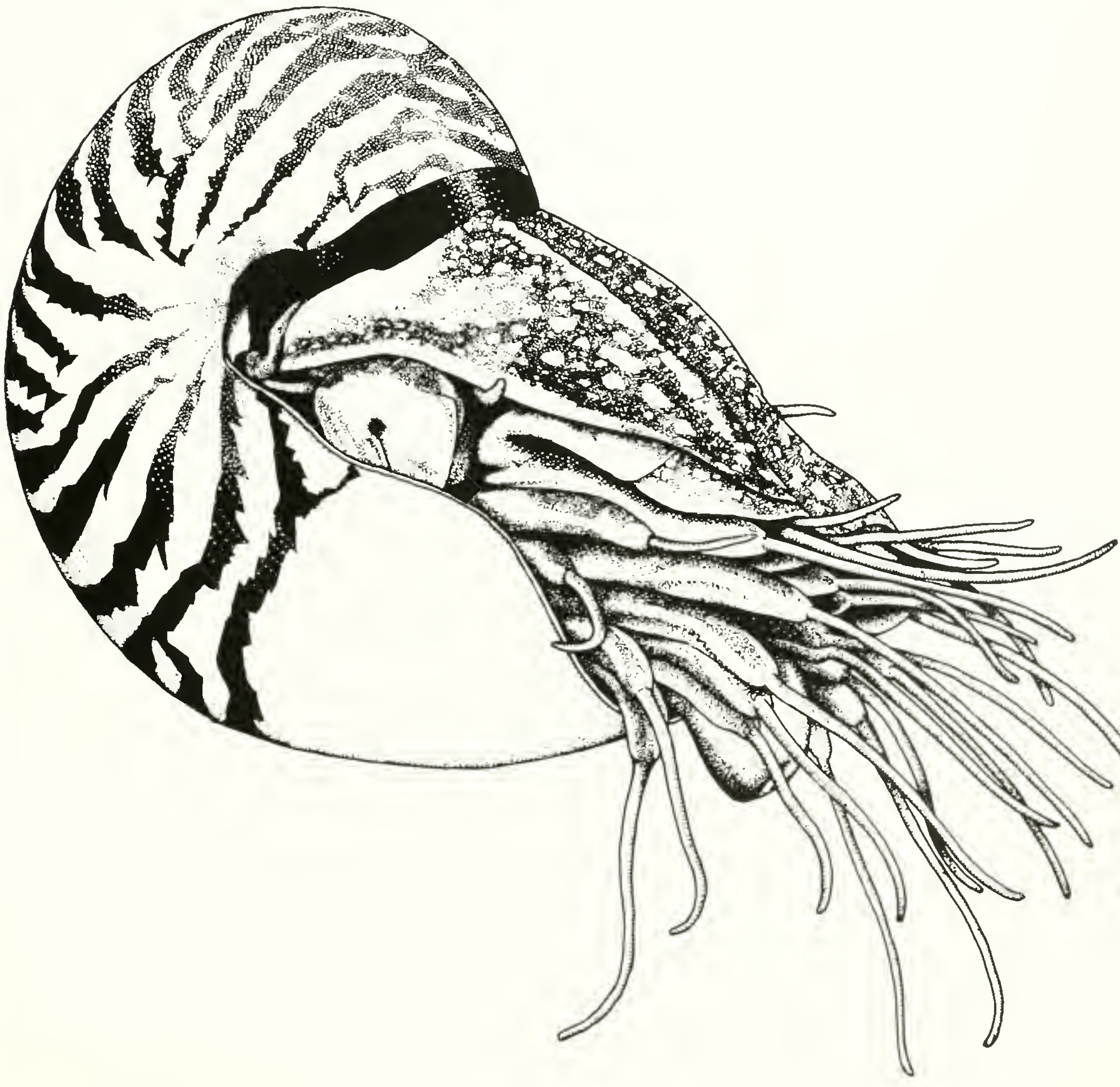

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NEW TAXA PROPOSED IN VOLUME 101 (1987)

GASTROPODA

THE NAUTILUS

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With the completion of Volume 100 of THE NAUTILUS, one dedicated to "all the molluscan enthusiasts, both private conchologists and professional malacologists, who founded and carried on for the last 100 years America's oldest journal devoted exclusively to the study of mollusks," Dr. R. Tucker Abbott retired as Editor-in-Chief. Under his direction, first as co-editor (1958–69) then as editor (1970–86), THE NAUTILUS has prospered and grown for nearly three decades. During his tenure as editor of THE NAUTILUS, R. Tucker Abbott also founded and edited *Indo-Pacific Mollusca* and *Monographs of Marine Mollusca*. In addition, Dr. Abbott has become the most prolific and widely published malacological author of his generation, having written many landmark books on American and worldwide mollusks, several of which have been published in multiple editions, as well as a number of monographs and numerous research papers. Having ushered THE NAUTILUS into its second century of publication, Dr. Abbott will continue to serve as Associate Editor, but will devote more time to writing. Like preceding editors of THE NAUTILUS, Dr. Abbott has earned an eminent position in the history of American malacology.

With a change in editorship, a number of other changes may be apparent, among them yet another change in journal size, a new cover and format, expanded instructions to authors, a larger panel of consulting editors, and a new publisher, Allen Press. For the new cover and format, we are greatly indebted to Hal Lewis Design, Inc. Finally, THE NAUTILUS, which had been privately owned in its first century of publication, is now published by Trophon Corporation, a non-profit corporation established to publish works on mollusks.

Despite these changes, the purpose of this publication, that of "giving information of vital interest to the student of Mollusca", remains the same. As it begins its second century of service to the malacological community, THE NAUTILUS will continue to meet ever higher standards in the publication of papers on all aspects of the biology and systematics of mollusks.

M. G. Harasewych
Editor

Tractolira germonae, A New Abyssal Antarctic Volute

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ABSTRACT

Tractolira germonae, a new species of volute, is described from abyssal depths along the Scotia Arc, and assigned to the previously monotypic genus *Tractolira* on the basis of shell and radular morphology. Anatomical characters of this new species support the inclusion of *Tractolira* in the subfamily Odontocymbiolinae, and suggest a close relationship between the subfamilies Odontocymbiolinae and Zidoninae.

INTRODUCTION

The United States Antarctic Research Program (USARP) has been conducting research, including the sampling of Antarctic and Subantarctic biotas for nearly three decades. A study of the abyssal gastropods collected by USARP has uncovered a number of specimens of a new species of volute, apparently endemic to the perimeter of the Scotia Sea. This species described herein is assigned to the previously monotypic genus *Tractolira* Dall, 1896. The inclusion of *Tractolira* in the subfamily Odontocymbiolinae by Weaver and duPont (1970:133) rested on the statement by Dall (1907:365) that the now lost radula of *T. sparta* Dall, 1896, the type species from the abyssal zone off western Central America, "is marked by the same tusk-like cusps as are found in *Miomelon*", one of the two genera originally included in the subfamily. A description of the anatomy serves as the basis for a discussion of the phylogenetic affinities of *Tractolira* and Odontocymbiolinae.

SYSTEMATICS

Family **Volutidae** Rafinesque, 1815
Subfamily **Odontocymbiolinae** Clench and Turner, 1964
Genus *Tractolira* Dall, 1896

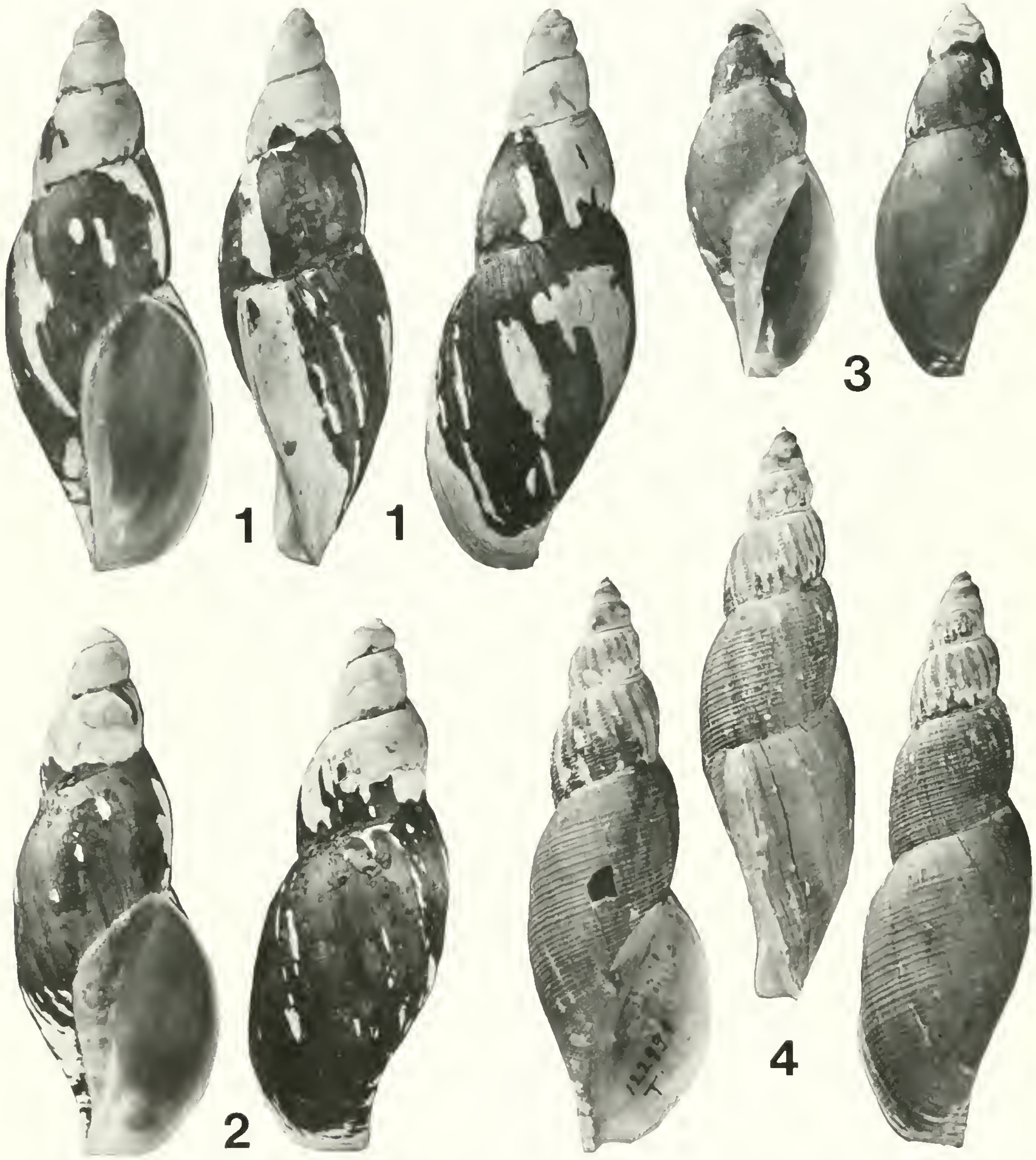
Tractolira germonae new species
(figures 1–3, 5–13; table 1)

Description: Shell (figures 1–3) to 60 mm, extremely thin, translucent, elongate, fusiform, eroded where not covered by periostracum (figures 5, 7). Protoconch badly eroded on all specimens, with vestiges of projecting calcarella at apex. Shell with up to five moderately convex whorls. Suture impressed. Spiral sculpture of 60–80 fine threads on body whorl, 20–30 on preceding whorls, decreasing in prominence with increase in shell size. Axial sculpture limited to fine growth striae. Aperture ovate. Outer lip smooth, slightly flared in larger specimens. Inner lip smooth, with thin transparent inductura along parietal region. Columella smooth, with raised white siphonal fold. Outer shell layer white to light tan, eroded areas of shell white, aperture white. Periostracum (figure 5) thin, greenish brown. Inner shell surfaces smooth, continuous.

Ultrastructure: Shell of three orthogonal layers of crossed lamellar crystals: outer layer 20 μm thick, with crystal faces perpendicular to growing edge; middle layer 120 μm thick, with crystal planes colabrally aligned; inner layer 12 μm thick, with crystal planes again perpendicular to growing edge. X-ray diffraction analysis showed shell to be composed almost exclusively (> 99%) of aragonite, with no significant amounts of calcite or vaterite.

External anatomy: Soft parts comprise three whorls, mantle cavity spans ½ whorl, kidney ⅓ whorl, digestive gland two whorls. Foot (L/W = 1.5) broad anteriorly, tapering posteriorly, with deep propodial mucous gland (figure 9, pmg). Operculum absent. Animal yellowish tan, without visible color pattern in alcohol-preserved material. Sole of foot deeply glandular, producing copious mucus. Siphon (figure 9, s) muscular, free, about ⅕ shell length. Two ventral appendages, equal in length, extend from base of siphon (figure 9, sa), one on each side of left cephalic tentacle (figure 9, t). Head broad, with short tentacles on each side of hood that extends over rhynchostome. Outer edges of tentacles with broad semicircular projections. Eyes absent.

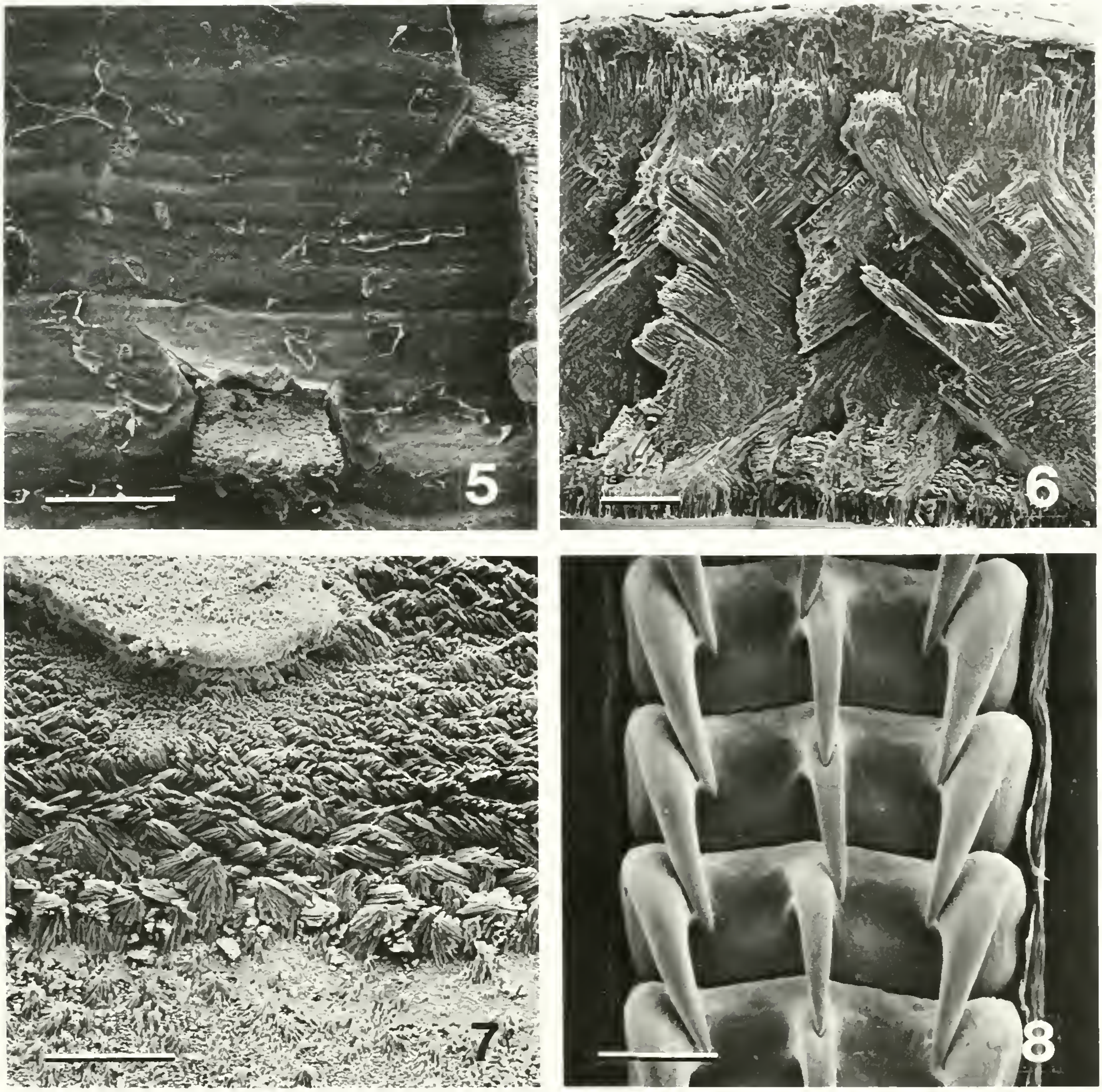
Mantle cavity: Arrangement of mantle cavity organs similar to that of *Alcithoe arabica* as described by Ponder (1970). Mantle edge thickened, muscular, smooth. Osphradium with 46 filaments below and 60 above osphradeal ganglion. Ctenidium, of about 200 filaments, slightly narrower (0.9 ×) and about 1.4 times as long as osphradium. Hypobranchial gland deeply glandular, producing purple secretion. Pericardium forms left rear



Figures 1–3. *Tractolira germonae* new species. **1.** Holotype, USNM 859076. **2.** Paratype 1, USNM 845611, both from Islas Orcada sta. 38, east of Candlemas Island, South Sandwich Islands, in 2,740–2,757 m. **3.** Paratype 5, USNM 845612, Islas Orcada sta. 51, south of Candlemas Island, South Sandwich Islands, in 2,248–2,402 m. **Figure 4.** *Tractolira sparta* Dall, 1896. Holotype, USNM 122999, Albatross sta. 3360, Gulf of Panama, in 3,058 m, sand bottom. All figures 1.5 ×.

wall of mantle cavity, ventricle diameter 2.5 × auricle diameter.

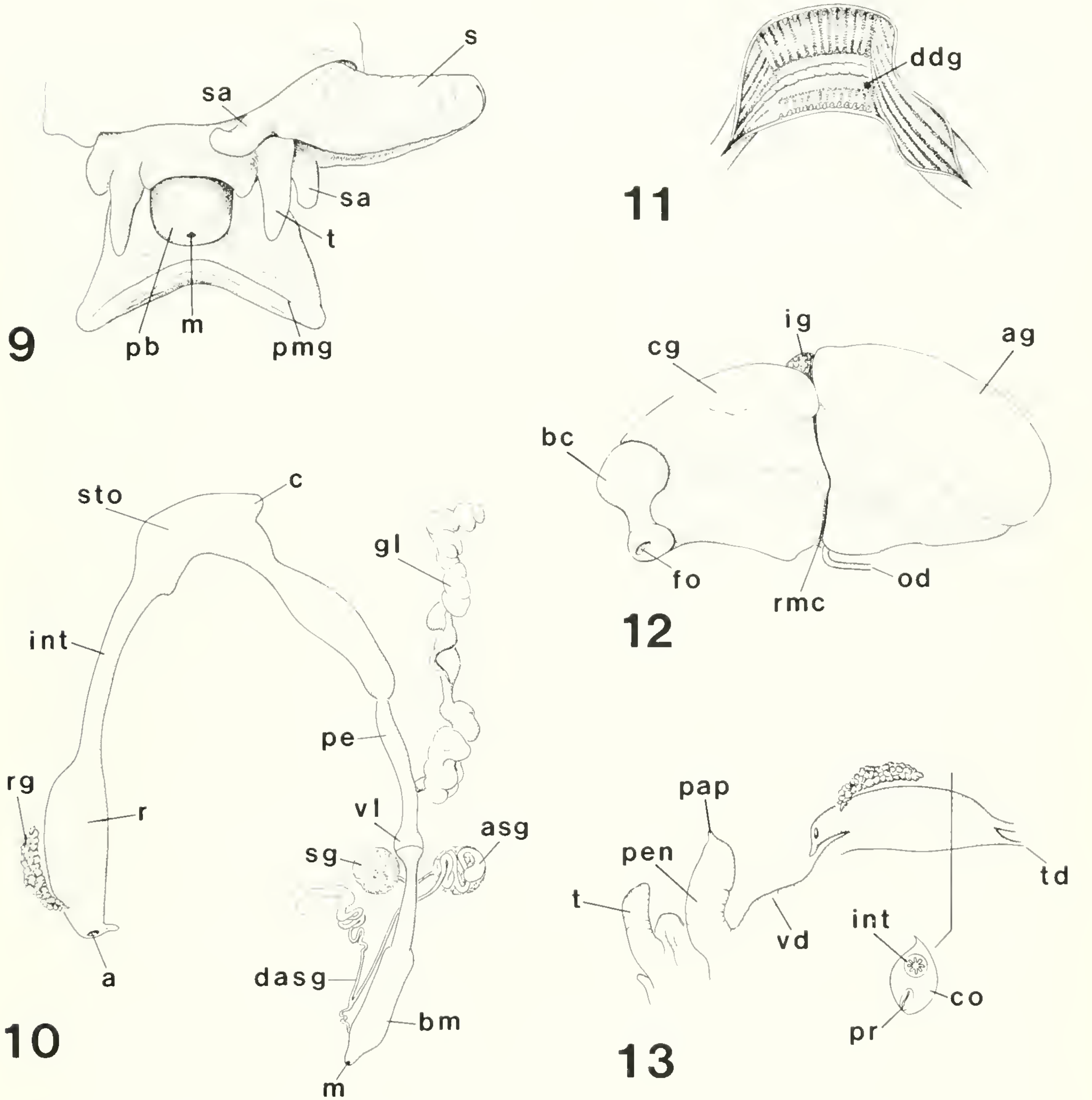
Alimentary system: Proboscis short, broad, pleurembolic, partially protruded in majority of specimens examined (figure 9, pb). Proboscis retractor muscles attached to walls of cephalic hemocoel. Mouth (figures 9, 10, m) triangular. Buccal mass (figure 10, bm) muscular. Radular ribbon short (5–7 mm), uniserial with 48–56 teeth, each with three tusk-like cusps. Central cusps



Figures 5–8. *Tractolira germonae* new species. **5.** Periostracum, scale bar = 200 μm. Note erosion of shell where not covered by periostracum. **6.** Shell ultrastructure, fracture surface parallel to growing edge, scale bar = 25 μm. **7.** Eroded surface of shell, scale bar = 80 μm. **8.** Radular ribbon, scale bar = 80 μm.

shorter and narrower than outer cusps (figure 8). Accessory salivary glands (figure 10, asg) wrapped tightly around salivary glands (figure 10, sg). Ducts of accessory salivary glands join (figure 10, dasg) before entering buccal cavity ventrally. Ducts of salivary glands run along the esophagus, entering buccal cavity dorso-laterally. Valve of Leiblein (figure 10, vl) large, nearly spherical. Gland of Leiblein (figure 10, gl), long, tubular, highly convoluted, fills posterior ⅔ of cephalic hemocoel. Posterior esophagus (figure 10, pe) reflected dorsally before joining U-shaped stomach. Section of stomach anterior to single duct from digestive gland (figure 11, ddg) tubular, with longitudinal folds. Posterior to digestive gland duct, stomach forms caecum (figure 10, c), becoming transversely pleated before joining intestine (figure 10, int). Intestine with longitudinal folds, expands into pink rectum (figure 10, r), with jade green anal gland (figure 10, ag) along distal ⅓ of its length. Anus (figure 10, a) with muscular rim and ventral papilla.

Female reproductive system: Ovary ascinous, whitish, on columellar side of digestive gland. Oviduct (figure



Figures 9–13. Anatomical features of *Tractolira germonae* new species. All figures 3.0 ×. **9.** Anterior view of animal. **10.** Alimentary system. **11.** Stomach, opened dorsally. **12.** Female glandular oviduct. **13.** Male pallial gonoduct.

a, anus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; bm, buccal mass; c, caecum; cg, capsule gland; co, connective tissue; dasg, duct accessory salivary gland; ddg, duct digestive gland; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; int, intestine; m, mouth; od, oviduct; pap, papilla; pb, proboscis; pe, posterior esophagus; pen, penis; pmg, propodial mucous gland, pr, prostate gland; r, rectum; rg, rectal gland; rmc, rear mantle cavity; s, siphon; sa, siphonal appendage; sg, salivary gland; sto, stomach; t, tentacle; td, testicular duct; vd, vas deferens; vl, valve of Leiblein.

12, od), thin, leading to rear of mantle cavity and entering anterior ventral edge of albumen gland (figure 12, ag), which forms right wall of kidney. Pallial oviduct is joined by the purplish ingesting gland (figure 12, ig) before expanding into capsule gland (figure 12, cg). Bursa copulatrix (figure 12, bc) forms blind muscular diverticulum between female opening (figure 12, fo) and capsule gland.

Male reproductive system: Testis yellowish tan, lines right side of digestive gland. Testicular duct tubular, passing along pericardium before entering mantle cav-

ity. Prostate gland (figure 13, pr) slit ventrally, spans posterior half of mantle cavity. Prostate and rectum surrounded by connective tissue (figure 13, co) to form cylindrical mass. Vas deferens (figure 13, vd) descends to mantle floor, forming groove with fused edges that runs to base of penis (figure 13, pen). Penis short, dorsoventrally flattened, reflected posteriorly, with terminal papilla (figure 13, pap). Penial duct as in *Alcithoe arabica* (Ponder, 1970: fig. 32).

Kidney: Kidney similar to that of *Alcithoe arabica* (Ponder, 1970: fig. 33), consisting of nephridial gland adjacent to pericardium, heavily pleated dorsal area, and ventral area with seven large lamellae. Latter two areas each fed by branch of the renal vein. Kidney opening over renal vein on left side of kidney. Reno-pericardial opening at anterior upper left corner of kidney.

Nervous system: Nervous system Type 2 (Ponder, 1970: 159), with supraesophageal and right pleural ganglia fused.

Etymology: This species honors Mrs. Raye N. Germon, Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, for her contributions to the study of Antarctic mollusks.

Type locality: East of Candlemas Island, South Sandwich Islands, 57°00.4′S, 27°10.1′W, in 2,740–2,757 m, Islas Orcada Cruise 575, sta. 38, May 22, 1975.

Holotype: USNM 859076, ♀, length 59.1 mm.

Paratypes: Paratypes 1–4, USNM 845611, from the type locality; paratypes 5–10, USNM 845612, paratype 11, ANSP A 11540, paratype 12, BM(NH) 198141, 57°22.6′S, 26°34.0′W, in 2,248–2,402 m, May 26, 1975, IO-575, sta. 51; paratypes 13–16, USNM 845613, 57°39.0′S, 26°00.4′W, in 2,380–2,609 m, May 27, 1975, IO-575, sta. 54; paratypes 17–19, USNM 845614, 56°29.5′S, 26°46.9′W, in 2,248–2,387 m, May 30, 1975, IO-575, sta. 63; paratypes 20–29, USNM 845615, paratypes 30–31, DMNH 169441, 56°03.5′S, 26°58.3′W, in 2,128–2,161 m, June 3, 1975, IO-575, 53°25.2′S, 45°17.0°W, in 2,632–2,691 m, June 12, 1975, IO-575, sta. 104.

Distribution: All live-collected specimens were taken off the South Sandwich Islands, with one record, based on shell fragments, from the Scotia Ridge. The confirmed bathymetric range for *T. germonae* is 2,161–2,740 m, with a mean station depth (n = 6) of 2,449 m. This species appears to be endemic to the Scotia Arc.

Ecology: All specimens of this abyssal species were taken on mud bottoms. Upper whorls of even the smallest specimens are eroded. The periostracum protects the shell from dissolution (figure 5), as this species lives below the aragonite compensation depth (Morse & Berner, 1979). A radular ribbon belonging to a naticid of the genus *Amauropsis* (Powell, 1951: fig. J) was found in the stomach of a dissected specimen.

Table 1. *Tractolira germonae* new species. Measurements of shell and radular characters. Linear measurements in mm. n = 10.

Character	$\bar{X}$	Range	SD
Shell length	50.0	35.9–59.2	6.9
Aperture length	27.0	21.4–30.1	3.2
$\frac{\text{Shell length}}{\text{Aperture length}}$	0.540	0.503–0.586	0.028
Total # whorls	4.75	4.25–5.00	0.25
Spire angle	31.8°	28.8°–37.6°	2.8°
Radular length	6.2	5.0–6.8	0.6
# Radular rows	52.4	48–56	2.7

Comparative remarks: *Tractolira germonae* differs from *T. sparta* Dall, its only living congener, in having a broader, less elongate shell with a proportionally larger aperture, in lacking axial ribs on the early whorls and in having broader, less pronounced spiral sculpture. Neither preserved material of *T. sparta* nor the radula described by Dall are available, and anatomical comparisons cannot be made, other than to note that the radula of *T. germonae* resembles that of *Miomelon philippiana* (Dall, 1896) (Pilsbry & Olsson, 1954: pl. 3, fig. 9), therein agreeing with Dall's (1907:365) description of the radula of *T. sparta*. The holotype of *Tractolira sparta* was illustrated by Dall (1908). The specimen figured by Weaver and duPont (1970: pl. 56 G, H) as the holotype is a paratype (USNM 123000) from Malpelo Island, Colombia. The holotype of *T. sparta* is figured herein (figure 4).

DISCUSSION

Clench and Turner (1964:170) erected the taxon Odontocymbiolinae, a replacement name for the subfamily Adelomeloninae Pilsbry and Olsson (1954), to include the South American genera *Odontocymbiola* and *Miomelon*. Although some species in these genera strongly resemble some members of the Zidoninae in shell form, Odontocymbiolinae can be readily identified by their characteristic radular teeth, which have "fang-like" denticles. Other characters that serve to differentiate the Odontocymbiolinae include the presence of the long, symmetrical siphonal appendages, tubular accessory salivary glands that are tightly wound around compact salivary glands, a vas deferens that forms a closed duct, a penis with closed duct and terminal papilla, and a stomach with a tubular anterior region. Although figured (pl. 82, figure 36), the last feature was not discussed by Clench and Turner (1964). Weaver and duPont (1970) provisionally included the abyssal eastern Pacific genus *Tractolira* and the Australian genus *Volutoconus* in Odontocymbiolinae, largely on the basis of radular morphology.

The inclusion of *Tractolira* in Odontocymbiolinae is further supported by features of the salivary glands, accessory salivary glands, stomach, and male reproductive

system. Although fang-like cusps are present in *Tractolira*, they are not as elaborately modified as in some other members of the subfamily (Weaver & duPont, 1970: figure 27). The protoconch of *Tractolira*, with its pointed calcarella, more closely corresponds to that of *Adelomelon ancilla* (Solander, 1786) (Clench & Turner, 1964: pl. 93), a member of the Zidoninae, than to those of Odontocymbiolinae (Clench & Turner, 1964: pl. 82, fig. 35). The penis of *Tractolira* has the duct and papilla of Odontocymbiolinae, but resembles that of Zidoninae in size and disposition.

In view of the numerous similarities in anatomy and shell morphology between the Zidoninae and Odontocymbiolinae (Clench & Turner, 1964), and because the character states that have been used to distinguish the Odontocymbiolinae are clearly derived from homologous features in the Zidoninae, it is suggested that these two subfamilies are sister groups, with the Odontocymbiolinae being derived from the Zidoninae, and that *Tractolira* is a primitive genus within the Odontocymbiolinae. Zoogeographic distributions of Recent species (Weaver & duPont, 1970) further suggest that the Zidoninae radiated in the Austral Province (Kauffman, 1973) during the Cretaceous, while the geographically more restricted Odontocymbiolinae evolved in the Weddellian Province (Zinsmeister, 1979, 1982) after the separation of New Zealand at the end of the Early Paleocene.

Dall (1907:365) proposed "*Voluta*" *alta* Sowerby, 1844, from shallow water early Tertiary deposits of Chile, as an ancestor of *Tractolira*. It is here proposed that the genus *Tractolira* colonized the abyssal regions of the Peru Basin during the early Tertiary, and that speciation of *T. germonae* is due to vicariance resulting from the displacement of tectonic fragments from the Pacific hinterland of the Andean-West Antarctic Cordillera into the southwestern Atlantic during the Cenozoic (Dalziel & Elliot, 1973).

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LITERATURE CITED

Clench, W. J and R D Turner. 1964 The subfamilies Volutinae, Zidoninae, Odontocymbiolinae and Calliotectinae in the western Atlantic. Johnsonia 4(43):129–180.

Dall, W. H. 1896. Diagnoses of new species of mollusks from the west coast of America. Proceedings of the United States National Museum 18:7–20.

Dall, W. H 1907. A review of the American Volutidae. Smithsonian Miscellaneous Collections 48(3):341–373.

Dall, W. H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in the charge of Alaxander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross" during 1891, Lieut. Commander Z. L. Tanner, U.S.N., Commanding, XXXVIII. and Reports on the scientific results of the expedition to the eastern tropical Pacific in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross", from October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., Commanding, XIV. Reports on the Mollusca and Brachiopoda Bulletin of the Museum of Comparative Zoology 43(6):205–487, pls. 1–22.

Dalziel, I W. D. and D. H Elliot. 1973 Evolution of the Scotia Arc and Antarctic Margin. *In:* Nairn, A. E. M. and F. G Stehli (eds.). The ocean basins and margins, vol. 1. The South Atlantic. Plenum Press, New York, NY, p. 171–245.

Kauffman, E. G. 1973. Cretaceous Bivalvia. *In:* Hallam, A. (ed.). Atlas of palaeobiogeography. Elsevier, Amsterdam, p. 353–383.

Morse, J. W. and R. C. Berner. 1979. Chemistry of calcium carbonate in the deep oceans. *In:* Jenne, E. A. (ed.). Chemical modeling in aqueous systems. American Chemical Society Symposium Series 93, Washington, DC, p. 499–535.

Pilsbry, H A. and A. A. Olsson. 1954. Systems of the Volutidae. Bulletins of American Paleontology 35(152):271–306.

Ponder, W. F. 1970. The morphology of *Alcithoe arabica* (Gastropoda Volutidae). Malacological Review 3:127–165.

Powell, A. W. B. 1951. Antarctic and Subantarctic mollusca: Pelecypoda and Gastropoda. Discovery Reports 26:47–196, pls. 5–10.

Sowerby, G. B. 1846. Descriptions of Tertiary fossil shells from South America. *In:* Darwin, C. Geological observations on South America, being the third part of the geology of the voyage of the Beagle, under the command of Capt Fitzroy, R N. during the years 1832 to 1836. Smith, Elder and Co., London, Appendix, p. 249–268, pls. 2–5.

Weaver, C. S. and J. E. duPont. 1970. Living volutes. Delaware Museum of Natural History, Greenville, DE, 375 p.

Zinsmeister, W. J. 1979. Biogeographic significance of the Late Mesozoic and Early Tertiary molluscan faunas of Seymour Island (Antarctic Peninsula) to the final breakup of Gondwanaland. *In:* Gray, J. and A. J. Bouchot (eds.). Historical biogeography, plate tectonics, and the changing environment. Oregon State University Press, Corvallis, OR, p. 349–355.

Zinsmeister, W. J 1982. Late Cretaceous–Early Tertiary molluscan biogeography of the southern circum-Pacific. Journal of Paleontology 56(1):84–102.

Anatomy of *Alaba* and *Litiopa* (Prosobranchia: Litiopidae): Systematic Implications

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ABSTRACT

Anatomical study of *Litiopa* and *Alaba* shows that these taxa differ from other cerithiaceans by a significant number of synapomorphies. These two taxa have been variously assigned to the Planaxidae, Litiopidae, Diastomidae, Rissoidae, Cerithiidae, and to a number of subfamilies of the latter family. Both genera are highly adapted to algal habitats and have a mesopodial mucous gland on the sole of the foot that produces long, anchoring mucus threads preventing dislodgement from the algae. They share similar taenioglossate radulae; many-whorled, ribbed protoconchs; nearly identical pallial oviducts; egg masses; and planktotrophic larvae. Both genera stand apart from other cerithiacean groups in having long, tapered, epipodial tentacles. The morphological evidence points to a close relationship between the two taxa and also supports their inclusion in the family Litiopidae Fischer, 1885.

INTRODUCTION

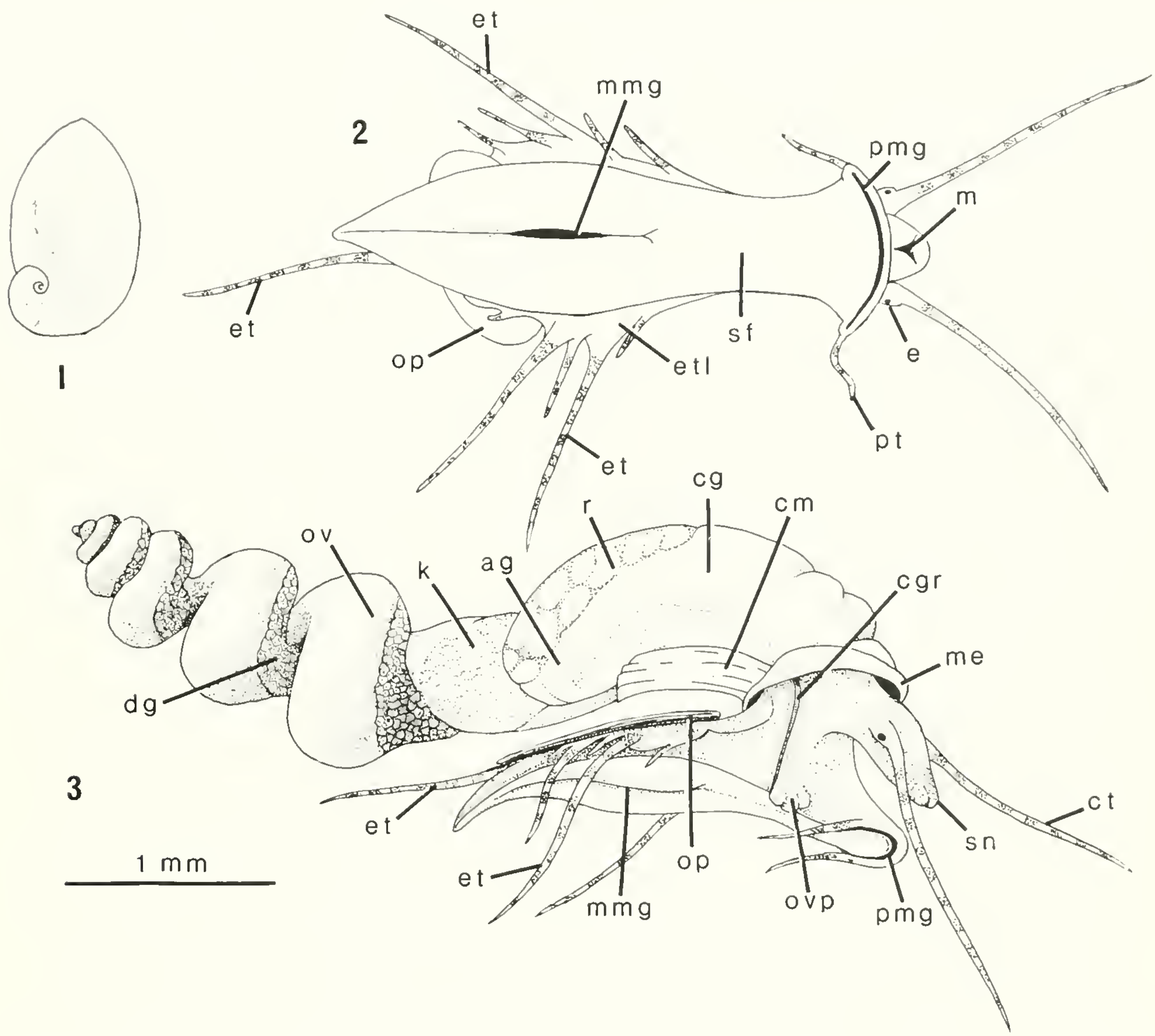
The higher taxonomic assignment of many small species of cerithiacean snails is controversial and frustrating. Convergent shell characters and lack of anatomical knowledge about the various taxa have resulted in an unstable classification. Moreover, many of the published systematic opinions about genera and families of cerithiaceans are based on vague, equivocal, conchological characters. I have discussed the taxonomic problems of small, heterogeneous cerithiacean taxa elsewhere (Houbrick, 1980:4–5, 1981:610–611). This paper deals with the anatomy of *Litiopa* Rang, 1829, *Alaba* H. and A. Adams, 1853, and several related taxa, and presents anatomical data for their natural systematic arrangement. *Litiopa*, while usually assigned to the family Litiopidae, has been thought to be related to the Planaxidae, Rissoidae, or Cerithiidae by various authors. *Alaba* has likewise been referred to the Cerithiopsidae, Planaxidae, Dialidae, Litiopidae, Diastomatidae, Cerithiidae, and to a number of subfamilies of the latter family. Bandel (1984:55) has discussed the confusing literature regarding the placement of *Alaba*. The status of a few other genera such as *Styliferina* A. Adams, 1860, and *Diffalaba* Iredale, 1936 remains uncertain. The genus *Diala* A. Adams, 1861 is frequently considered a close relative of both *Alaba* and *Litiopa* and has been grouped with them (A. Adams, 1862; Smith, 1875:538) or placed in its own family, Dialidae (Hornung & Mermoud, 1928). Dall (1889:258) suggested that *Alaba* was related to *Bittium* Gray and *Diastoma* Deshayes. Other workers, such as Wenz (1938) and Franc (1968), have included *Finella* A. Adams, *Alabina* Dall, and *Alaba* with the Diastomatidae. A summary of the various taxonomic allocations of *Alaba* and *Litiopa* is presented in table 1. Most workers have referred the two taxa to the subfamily Litiopinae and placed this group under the Cerithiidae Bruguière, 1789.

MATERIALS AND METHODS

Living specimens of *Litiopa melanostoma* Rang, 1829 and *Alaba incerta* (Orbigny, 1842) were studied at the Smithsonian Marine Station at Link Port, Ft. Pierce, Florida during January, February, and April of 1986. *Litiopa melanostoma* was collected offshore on *Sargassum* weed. *Alaba incerta* was collected from intertidal marine grass beds in St. Lucie Inlet, Florida, and on shallow water grass beds around Peanut Island in Lake Worth, Riviera Beach, Florida. Living snails were maintained in petri dishes of sea water and relaxed in a 10% $MgCl_2$ solution for study under a binocular dissecting microscope. Snails were preserved in Bouin's seawater fixative, embedded in paraffin, sectioned at 7 μm, and stained with Alcian blue-PAS and counterstained in hematoxylin (Humason, 1962:269). Critical point dried animals extracted from shells, radular ribbons, and protoconchs were examined under a Novascan-30 scanning electron microscope to determine microscopic anatomical features. Protoconchs of some *Australaba* and *Finella* species were also compared with those of litiopids.

MORPHOLOGY

Shell morphology: Members of both genera are small, not exceeding 25 mm in length, and have moderately turreted, conical, thin, nearly transparent shells. The shell



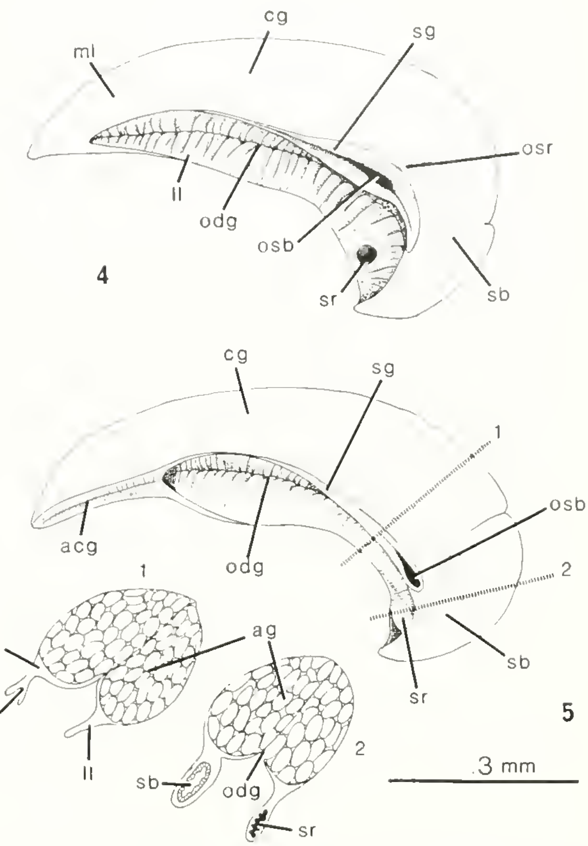
Figures 1–3. Animal of *Alaba incerta*. **1.** Operculum, showing sinuous attachment ridge, by transparency. **2.** Ventral view, showing sole of foot and disposition of epipodial tentacles. **3.** Side view of female, showing ciliated groove and ovipositor on right side of head-foot (bar = 1 mm). ag = albumen gland; cg = capsule gland; cgr = ciliated groove; cm = columellar muscle; ct = cephalic tentacle; dg = digestive gland; e = eye; et = epipodial tentacle; etl = epipodial tentacular lobe; k = kidney; m = mouth; me = mantle edge; mmg = mesopodial mucous gland; op = operculum; ov = ovary; ovp = ovipositor; pmg = propodial mucous gland, pt = propodial tentacle; r = rectum; sn = snout; sf = sole of foot.

of *Alaba* (figure 11) differs from that of *Litiopa* (figure 9) in being longer and in having irregularly distributed, wide varices and a taller, more turreted apex. In *Litiopa*, the whorls are more inflated and fewer in number than in *Alaba*, and the shell is tan-yellow while that of *Alaba* is vitreous and white. *Litiopa* has a wider aperture and a weak tooth at the base of the columella. Both taxa have tiny brown subsutural spots and flammules, but *Alaba* also has weak, spiral bands of tan spots. *Litiopa* and *Alaba* have nearly identical protoconchs comprising 3.5–4 whorls (figures 8, 10). Protoconch I is smooth (pitted under high magnification) while protoconch II is sculptured with numerous axial riblets divided by a thin spiral thread from a band of subsutural plaits. Microscopic spiral lines lie between the axial riblets in *Litiopa* (figure 8). A good figure of *Litiopa melanostoma* and its protoconch has been given by Okutani *et al.* (1983: 24, figs. 1–5). Robertson (1971:5, pls. 2, 3) presented detailed figures of the protoconchs of *Alaba incerta* and *Litiopa melanostoma*. The periostraca of both taxa are thin and transparent. The ovate, paucispiral opercula are completely transparent and have eccentric nuclei in both taxa. Only the portions of the opercula beneath the nuclei are attached to the metapodia by fine sinuous ridges (figure 1). This opercular attachment scar is clearly depicted by Robertson (1971:pl. 4, fig. 16), who noted

the similarity of the opercula of both taxa. A ridge-like attachment scar is also described for *Alaba goniochila* by Kosuge (1964:36, fig. 6).

External anatomy: *Litiopa* and *Alaba* are very active snails and move about quickly in the algae or on the underside of the surface film of the water, on which they glide shell down by means of their long foot. Externally, *Litiopa* is yellow with a pale foot while *Alaba* has a whitish base color flecked with olive brown and red spots. The slender cephalic and pedal tentacles are striped with reddish brown in *Alaba*. A conspicuous feature in both genera is the long, narrow, active foot which is used to climb about algal filaments and fronds. A very deep, anterior propodial mucous gland lies at the leading edge of the sole (figures 2, 3, 7, 15, pmg) and a large, mesopodial mucous gland is centrally located at the posterior of the sole (figures 2, 3, 7, 12, 15, mmg). The propodial mucous gland produces a sheet of mucus that moves posteriorly along the sole of the foot. Scanning electron micrographs of critical point dried snails show that the sole of the foot is covered with long, dense, cilia (figure 17). The mesopodial mucous gland is defined by a slit-like groove (figures 2, 3, 7, 12, 15, mmg) that produces a strong mucus thread attaching the snail to the substrate or surface film of the water. If accidentally pulled or dislodged from their algal habitat, litiopids cling to the mucus thread in spider-like fashion, employing the foot and mouth to crawl back and reestablish themselves. The mucus thread is quite strong and tensile. The mesopodial mucous gland occurs in both genera, but is especially well-developed in the pelagic snail, *Litiopa*. Neither of these anatomical features was noted by Kosuge (1964), although he depicted a longitudinal groove on the sole. A. Adams (1862) was the first to note the mesopodial mucous gland in *Alaba*, but his comments on the gland and its use in the spinning of mucus threads have been overlooked by subsequent workers. He also remarked that *Alaba* was similar to *Litiopa* in this respect. A small, median, mesopodial mucous gland that opens by a short duct to the posterior portion of the sole also occurs in the Turritellidae (Randles, 1900:57).

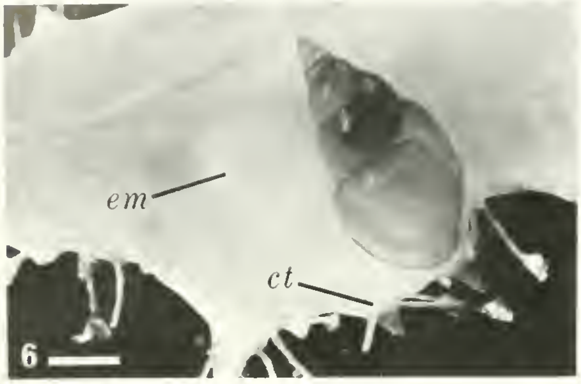
Another conspicuous feature in litiopids, and especially in *Alaba*, is the presence of long epipodial tentacles along the sides of the foot (figures 2, 3, 15, 16, et), as noted by A. Adams (1862). The leading edge of the propodium has a pair of small, short tentacles, one on each side (figures 2, 3, pt). A lobe of epipodial tissue runs along the postero-lateral part of the metapodium, adjacent to the edge of the sole and supports the epipodial tentacles and operculum (figure 2, etl). The major epipodial tentacles are long and tapered. A pair occurs on the left side of the foot and a single one is on the right side. A single tentacle is also at the posterior of the foot. Other smaller tentacles flank the major tentacles. When *Alaba* is viewed dorsally, the long right epipodial tentacle emerges from the exhalant siphon. Epipodial and cephalic tentacles have circular ridges along their lengths (figures 15, 16, et, ct). These ridges are not seen

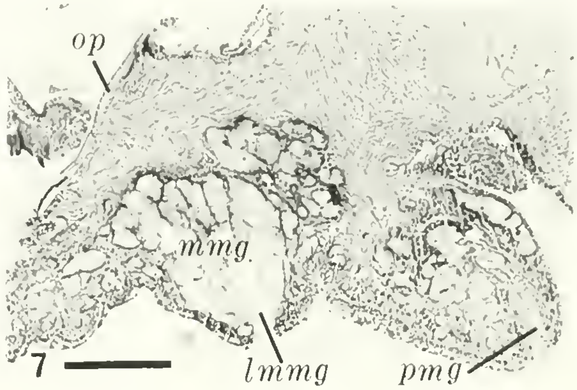


Figures 4, 5. Litiopid pallial oviducts (distal end on left; bar = 0.3 mm). **4.** *Litiopa melanostoma*. **5.** *Alaba incerta* (dotted lines 1 and 2 represent cuts corresponding to diagrammatic cross sections 1 and 2). acg = anterior ciliated groove; ag = albumen gland, cg = capsule gland; ll = lateral lamina; ml = medial lamina; odg = oviductal groove; osb = opening to spermatophore bursa; osr = opening to seminal receptacle; sb = spermatophore bursa; sg = sperm groove; sr = seminal receptacle

on living snails and may be the result of contraction of the tentacles. A. Adams (1862) described a pair of epipodial tentacles on each side of the foot and a posterior pair in *Alaba picta* A. Adams, 1861. Kosuge (1964:36, figs. 1, 2) illustrated slender epipodial tentacles extending well beyond the shell margin of *Alaba goniochila*. In *Litiopa*, the epipodial tentacles are much shorter and less conspicuous.

The small head has a moderately extensible bilobed snout and a pair of long, tapered cephalic tentacles (figures 2, 3, 6, 15, ct) that are extremely retractile and touch the substrate alternately while the snail is crawling. The black eyes are surrounded by yellow pigment and located on the outer edge of the tentacular peduncle (figures 2, 3, e). The eyes are tiny and the tentacular bases have no peduncular bulge in *Litiopa*. The mantle edge of litiopids is smooth and bifurcate (figures 3, 15, me). Females have a ciliated groove (figures 3, 15, cgr) that emerges from the distal pallial oviduct, runs down the right side of the head-foot, and ends at the foot edge





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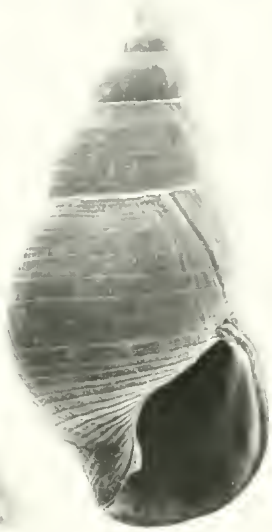

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Figure 6. *Litiopa melanostoma* and egg mass on *Sargassum* leaf (ct = cephalic tentacle; em = egg mass). **Figure 7.** Sagittal section through foot of *Alaba incerta*, showing operculum (op), mesopodial mucous gland (mmg), duct opening (lmmg), and propodial mucous gland (pmg) (bar = 0.5 mm). **Figure 8.** Protoconch of *Litiopa melanostoma*, showing sinusigeral notch (bar = 80 μm). **Figure 9.** Adult shell of *Litiopa melanostoma* from off Ft. Pierce, Florida (length 7 mm). **Figure 10.** Protoconch of *Alaba incerta*, showing sinusigeral notch (bar = 80 μm). **Figure 11.** Adult shell of *Alaba incerta* from St. Lucie Inlet, Florida (length 15 mm). **Figure 12.** Transverse section of *Alaba incerta* showing buccal mass (bm), foot (f), large mesopodial mucous gland (mmg), and lumen of duct (lmmg) (bar = 0.5 mm). **Figure 13.** Radula of *Litiopa melanostoma* (bar = 20 μm). **Figure 14.** Details of rachidian, lateral, and marginal teeth of *Litiopa melanostoma* (bar = 16 μm).

adjacent to the sole, where a fleshy glandular pad, the ovipositor (figure 3, ovp), is situated. The ovipositor is especially well-developed in *Litiopa*. Okutani *et al.* (1983:24, fig. 6) depicted the groove but not the ovipositor.

The coils of the body whorl comprise the digestive gland, gonad, stomach, and kidney and are typically cerithioid in groundplan.

Mantle cavity organs: Litiopid snails have a deep mantle cavity dominated by a large ctenidium. A ridge-like monopectinate osphradium extends the full length of the ctenidium. Ctenidial filaments are long, tapered, triangular, and have many long cilia. Similar observations were made by Kosuge (1964:34) on *Alaba goniochila*. The narrow hypobranchial gland is thick, and in *Alaba* secretes an iridescent green substance when the snail is injured or irritated. The rectum is thin walled and produces large ovoid fecal pellets that are tapered at one end. The glandular pallial gonoducts are large and thick in females but small and thin in males.

Alimentary tract: The buccal mass of litiopids is large in relation to the snout size and has a pair of semicircular jaws. The radular ribbon of *Alaba* comprises 35–40 rows of teeth (n = 6) and is about one-fourth the shell length. The large buccal mass of *Alaba* was also noted by Kosuge (1964:34). The radulae of *Alaba* (figures 18–20) and *Litiopa* (figures 13, 14) are taenioglossate (2+1+1+1+2) and typically cerithioid, closely resembling the radulae of Cerithiidae in overall morphology. The rachidian tooth of *Alaba* (figure 19, r) is wider than long, has a straight anterior front, and an hourglass-shaped basal plate with a prominent central triangular buttress. This hourglass shape is also found in some genera and species of the Cerithiidae (Houbrick, 1980). The cutting edge of the rachidian has a sharply pointed central cusp flanked on each side by a pair of smaller denticles. The lateral tooth (figure 19, l) is trapezoidal and has a basal plate with a long lateral basal extension and a strong, ventral, inner buttress. The cutting edge has a long central cusp, one inner denticle, with two outer denticles in *Alaba* (figure 19, l), and two to four in *Litiopa* (figure 13). The marginal teeth of both genera (figures 13, 14, 18–20) are equal in length, scythe-shaped, and have cusped, spoon-like tips. The inner marginal tooth is about twice as broad as the outer and has two inner denticles, a long terminal cusp, and one outer denticle. The narrow outer marginal has 4–5 inner denticles in *Alaba* (figure 20), 8–9 in *Litiopa* (figure 13), a long terminal cusp, and a smooth outer edge. The radula of *Alaba incerta* has been described and figured in detail by Bandel (1984:39–40, fig. 71, pl. 4, figs. 1, 9).

The mouth (figures 2, 15, m) and oral cavity are large and manipulate long strands of filamentous algae in *Alaba* and large *Sargassum* particles in *Litiopa*. The radula of *Alaba goniochila* is very similar to that of *Alaba incerta* (Kosuge, 1964:36, figs. 7–10).

Litiopids have a pair of tubular, uncoiled salivary glands that originate well behind the nerve ring and pass through it before emptying into the buccal cavity. Salivary gland tubes are thicker in *Litiopa* than in *Alaba*. A large esophageal gland, formed by outpocketing of the lateral walls of the midesophagus, is present in *Litiopa*. This was also found in *Alaba incerta* and was noted by Kosuge (1964:34) in *Alaba goniochila*. The stomach of litiopids has a large central ridge, a gastric shield, and a short style sac. Although not seen in dissections, histological sections show that a crystalline style is present. The stomach of *Alaba goniochila* has been depicted by Kosuge (1964:36, fig. 5), and is similar to *Alaba incerta*. Sections show that the major typhlosole extends well into the proximal intestine.

Reproductive tract: *Litiopa* and *Alaba* are typically cerithiacean in having open gonoducts and aphallate males. The pallial oviducts of both taxa consist of a thick-walled, slit tube attached along its dorsal side to the mantle wall (figures 4, 5). It comprises two laminae, a lateral one attached along its width to the mantle wall (figures 4, 5, ll) and a medial, free lamina (figures 4, 5, ml). Along the longitudinal base of the laminae is the oviductal groove, which is wide and shallow (figures 4, 5, odg). The bulk of the pallial oviduct is dominated by a large swollen, proximal albumen gland (figure 5, ag) and by the adjacent distal capsule gland (figures 4, 5, cg). These glands have a mucus-like consistency and quickly swell with water when cut or injured. The albumen gland is more opaque than the capsule gland and stains a deep blue in section. The free medial lamina has a sperm groove along its median edge (figures 4, 5, sg) that enters into a small, proximal bursa (figures 4, 5, sb). In *Litiopa*, the bursa leads into a small pouch that appears to have a tiny opening on the inner side of the medial lamina (figure 4, osr). In the lateral lamina, immediately adjacent to this opening, is a pit-shaped pouch that is probably the seminal receptacle (figure 4, sr). The seminal receptacle is a round, deep chamber in *Litiopa* (figure 5, sr) while it is a compact pouch in *Alaba*.

Eggs and larvae: The egg masses of *Litiopa* and *Alaba* are similar, forming flattened, gelatinous, clockwise spirals comprising one to four tight turns. Spawn masses of *Alaba* vary in size but average about 4.8 mm in diameter (n = 6). Unwound, an egg mass of this dimension comprises a ribbon 18.5 mm long and 0.35 mm wide. A ribbon has 2–3 layers of very small eggs, about six across the ribbon width, and contains about 4,800 eggs. Each egg is 60 μm in diameter and is enclosed in a clear hyaline capsule about 80 μm in diameter. This, in turn, is enclosed in an irregularly shaped gelatinous chamber about 0.13 mm across. The jelly chambers are covered in a gelatinous sheet forming a ribbon which is wound into a spiral which slightly overlaps the previous spirals. Jelly chambers and their enclosed eggs are tightly packed in the central region of the ribbon. The egg mass of *Litiopa* is deposited on *Sargassum* fronds (figure 6, em) and is similar to but smaller than that of *Alaba*, measuring about 2.5 mm in diameter and having fewer, broader spirals.

Egg masses of *Alaba picta* have been depicted by Habe (1960:122, fig. 4; cited as *Australaba picta*), Amio (1963:306, fig. 26), and Bandel (1976:262). Their figures conform with observations of *Alaba incerta* spawn. The egg mass of *Litiopa* has been poorly figured by Lebour (1945:467–468, fig. 8a) who described it as a flat circular mass. She did not note the spiral arrangement of the jelly ribbon.

Development is rapid in both genera, the trochophore stage being attained in 2 days and early veliger stages within 3 days. Hatching takes place in about 6 days and is preceded by disintegration of the egg mass. Freed veligers are active swimmers and have a large bilobed velum with long cilia and a transparent shell. Lebour (1945:467, fig. 8c) depicted velar lobes of very unequal size in *Litiopa* and stated that it is one of the commonest veligers in open water plankton. The larval shell of *Alaba* has a reddish brown columella. Bandel's (1976:262) observations on *Alaba* from Santa Marta, Colombia, are essentially in agreement with mine. He noted that it takes a female about 90 minutes to produce a 2 cm long ribbon.

The many-whorled, sculptured protoconchs with deep sinusigeral notches (figure 10) seen on the apex of adult snails of both taxa indicate a long planktotrophic phase before settlement. The protoconchs of *Litiopa* and *Alaba* are nearly identical in having many axial riblets. The protoconch of *Litiopa* has microscopic spiral lines between the riblets and comprises about five sculptured whorls (figure 8) while in *Alaba*, there are only three whorls (figure 10). The larger protoconch of *Litiopa* indicates a long planktonic phase that is reflected in the pan-tropical distribution of this pelagic species. Robertson (1971:5) noted the close resemblance between the protoconchs of *Litiopa* and *Alaba* and pointed out that full grown larval shells of *Litiopa* are larger than those of *Alaba*. He also noted the spiral lines ("crests") between the axial ribs on *Litiopa* protoconchs. The litiopid protoconch is distinctive among cerithiaceans and appears to be a good familial taxonomic character.

Nervous system: Litiopids have an epiathroid nervous system. A statocyst occurs on the posterior of each pedal ganglion. The cerebral ganglia are joined by a very short commissure and the pleural ganglia are closely joined to the cerebrals. The subesophageal ganglion, although completely separated from the left pleural ganglion, is only separated from it by a very short connective. Zygoneury does not occur. The supraesophageal ganglion is embedded in the left wall of the cephalic cavity. The RPG ratio (Davis *et al.*, 1976:263) was 0.43 ($n = 2$) in *Litiopa*, indicating a tightly organized nerve ring. This is the lowest ratio observed among the Cerithiacea, but the low value may be a reflection of the small body size of litiopids, and its significance is questionable.

SYSTEMATIC CONCLUSIONS

Below is a family diagnosis and synonymies suggested for the genera *Litiopa* and *Alaba*. The synonymy for *Alaba* is tentative and needs confirmation by careful conchological and anatomical examination of the type-species of each taxon.

Family **Litiopidae** Fischer, 1885

Diagnosis: Shell small, thin, having weak, shallow anterior canal and protoconch sculptured with numerous axial riblets and subsutural plaits. Animal with epipodial tentacles, smooth mantle edge, mesopodial mucus gland, ridge-like osphradium, large esophageal gland, short sperm gutter, and seminal receptacle in lateral lamina of pallial oviduct.

Genus *Litiopa* Rang

Diagnosis: Shell moderately turreted, yellow-brown in color, with inflated, weakly sculptured whorls and ovate aperture with weak tooth at base of columella. Protoconch sculptured with microscopic spiral lines between axial riblets. Animal yellow with well-developed ovipositor on right side of foot in females. Seminal receptacle a deep round chamber in posterior lateral lamina of pallial oviduct.

Litiopa Rang, 1829:306. Type-species: *Litiopa melanostoma* Rang, 1829, by SD, Nevill, 1884.

Bombyxinus Belanger *in* Lesson, 1835:32. Type-species: *Litiopa melanostoma* Rang, 1829, by OD.

Bombycinus (emend. pro *Bombyxinus* Belanger, 1835) Agassiz, 1846:104.

Genus *Alaba* H. and A. Adams

Diagnosis: Shell vitreous, white, weakly sculptured, with quadrangular aperture and very weak anterior canal; thick varices present on several whorls. Protoconch with numerous axial riblets. Seminal receptacle a compact pouch in posterior lateral lamina of pallial oviduct.

Alaba H. and A. Adams, 1853:241. Type-species: *Rissoa melaneura* C. B. Adams, 1850, by SD (Nevill, 1885).

Gibborissoa Cossmann *in* Sacco, 1895:34. Type-species: *Bulimus costellata* Grateloupe, 1828, by OD.

Diffalaba Iredale, 1936:290. Type-species: *Diffalaba opiniosa* Iredale, 1936, by OD.

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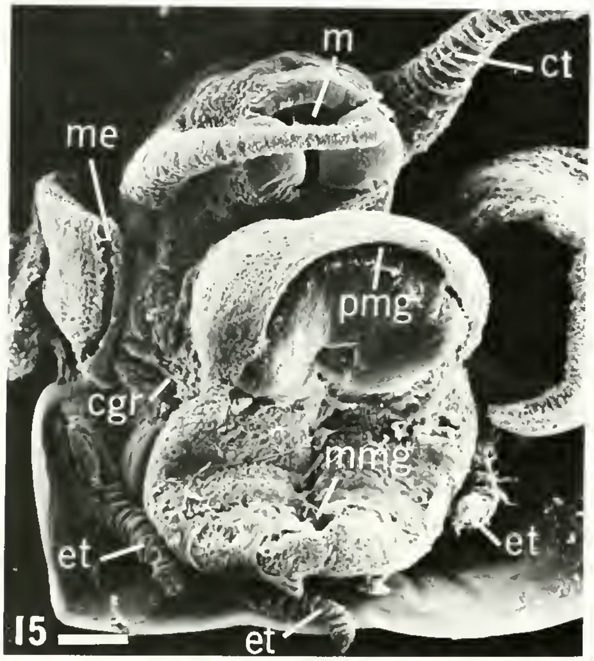
Figures 15–20. *Alaba incerta*, animal and radula. **15.** Critical point dried head-foot, showing sole and mucous glands. ct = cephalic tentacle; et = epipodial tentacle; cgr = ciliated groove; m = mouth; me = mantle edge; mmg = mesopodial mucous gland, pmg = propodial mucous gland (bar = 240 μm). **16.** Detail of epipodial tentacles on critical point dried snail. et = epipodial tentacle (bar = 40 μm). **17.** Dense cilia on sole of foot (bar = 4 μm). **18.** Radula ribbon with marginal teeth spread back (bar = 40 μm). **19.** Detail of rachidian (r) and lateral (l) teeth (bar = 20 μm). **20.** Inner and outer marginal teeth (bar = 20 μm).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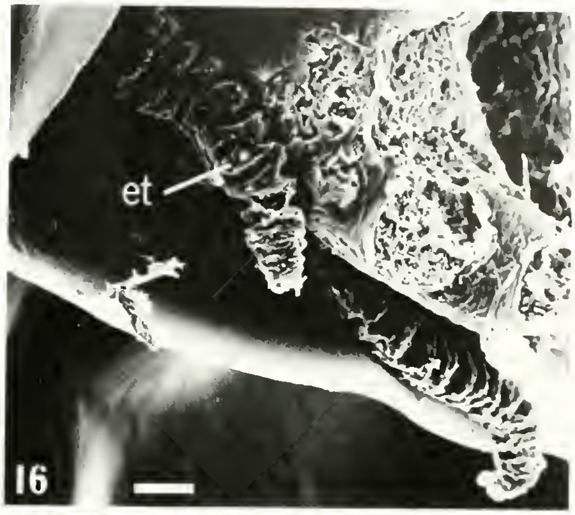
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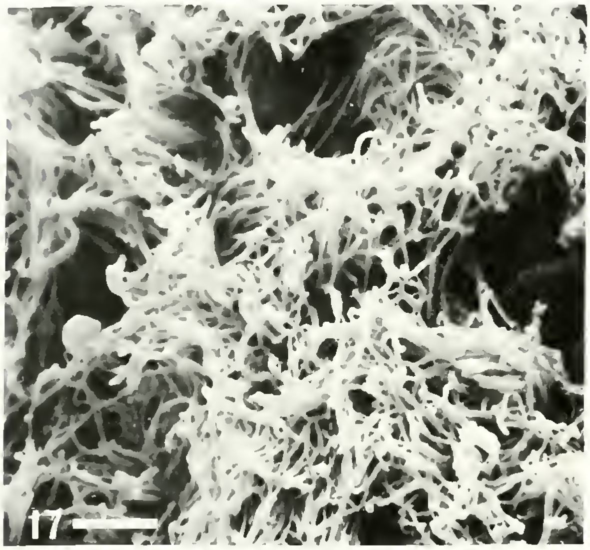
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Table 1. Taxonomic allocations given to *Litiopa* and *Alaba*.

Genus	Subfamily	Family	Citation
Litiopa		Planaxidae	Tryon (1882:246–247)
		Litiopidae	Fischer (1887:718–719)
	Litiopinae	Planaxidae	Cossmann (1906:196–197)
	Litiopinae	Cerithiidae	Thiele (1929:210–211)
	Litiopinae	Cerithiidae	Wenz (1938:753)
	Litiopinae	Cerithiidae	Franc (1968:281)
	Litiopinae	Cerithiidae	Keen (1971:415–416)
	Litiopinae	Cerithiidae	Abbott (1974:108)
		Litiopidae	Iredale and McMichael (1962:43)
Alaba		Planaxidae	Tryon (1882:246–247)
		Cerithiopsidae	H. and A. Adams (1853:239)
	Litiopinae	Cerithiidae	E. A. Smith (1875:537)
	Litiopinae	Cerithiidae	Thiele (1929:210–211)
	Litiopinae	Cerithiidae	Wenz (1938:753)
	Litiopinae	Dialidae	Iredale and McMichael (1962:43)
	Diastominae	Cerithiidae	Keen (1971:415–416)
	Cerithiopsinae	Cerithiidae	Abbott (1974 108)
		Diastomidae	Kilburn and Rippey (1982:537)
		Rissoidae	Laseron (1956:459)

Obstopalia Iredale, 1936:299. Type-species: *Obstopalia lixa* Iredale, 1936, by OD.

Australaba Laseron, 1956:459. Type-species: *Australaba bowenensis* Laseron, 1956, by OD

Styliferina A. Adams, 1860:335. Type-species: *Styliferina orthochila* A. Adams, 1860, by OD.

Dialessa Iredale, 1955:81. Type-species: *Alaba translucida* Hedley, 1906, by OD.

DISCUSSION

No comprehensive anatomical studies of *Litiopa* or *Alaba* have previously been made. The earliest descriptions of the superficial anatomy and habits of *Alaba* were by A. Adams (1862), who described the animal of *Alaba picta*, a Japanese species living in shallow water *Zostera* beds. Adams (1862) pointed out the unusual features, such as epipodial tentacles and the mesopodial mucous gland, and noted that *Litiopa* shared these characters. He considered *Diala* and *Styliferina* as subgenera of *Alaba* and grouped all three in the family Litiopidae. His paper has been overlooked by subsequent workers. The genus *Styliferina* was originally described by A. Adams (1860:335), who later considered it a subgenus of *Alaba* A. Adams, 1862.

There are two short recent papers on the anatomy of litiopids: one by Kosuge (1964) on *Alaba goniochila*, and a few brief notes on *Litiopa melanostoma* by Okutani *et al.* (1983). Ponder (1985:104) has noted that in Kosuge's (1964) paper, *Alaba goniochila* is incorrectly cited as *Diala goniochila*, and likely to be overlooked in the literature for this reason. Furthermore, this paper may mislead others to include the genus *Diala* with the Litiopidae. There can be no doubt that the species shown by Kosuge (1964) is an *Alaba* and not a *Diala*, for his description and figures unequivocally depict epipodial tentacles. I was previously misled by this paper when I incorrectly stated that *Diala* snails have epipodial tentacles (Houbrick, 1980:4). Living *Diala* species examined in Queensland, Australia, did not have epipodial tentacles. It is thus clear that *Diala* is not closely related to *Litiopa* or *Alaba* and should not be referred to the Litiopidae. In the brief paper by Okutani *et al.* (1983) on *Litiopa*, only a radular drawing and a sketch of the head-foot were presented. The authors did not note the epipodial tentacles or the metapodial mucous gland, and incorrectly stated that there was no modification for pelagic life.

Although only two genera are now unequivocally included in Litiopidae, other species and genera of small cerithiaceans may prove to be members of this group when their anatomy is better studied. The type of *Finella xanthacme* (Melvill, 1904) [= *Obtortio*] has a protoconch like that of *Litiopa*, but no epipodial tentacles (Ponder, personal communication). Ponder (1967:197, pl. 10, figs. 7–9) has depicted the radula and operculum of *Alaba* (*Dialessa*) *translucida* (Hedley), strongly suggesting that the subgenus *Dialessa* is a litiopid. He later considered *Dialessa* to be a litiopid (Ponder, 1985:104) and has stated that *Dialessa* has an *Alaba*-like animal (Ponder, personal communication).

Much of the anatomy of litiopids is similar to that of the cerithiids. The long extensible foot observed in litiopids also occurs in *Bittium* species from similar algal habitats. The ovate, paucispiral operculum with eccentric nucleus is also like that of *Cerithium* species. The ciliated groove and ovipositor on the right of the foot of females occur in Cerithiidae, in the genera *Cerithium*, *Bittium* (Marcus & Marcus, 1964:507), and *Rhinoclavis* (personal observation); in Potamididae, in *Batillaria* (personal observation) and *Cerithidea* (Houbrick, 1984: 3); and in the Modulidae and Thiaridae (Houbrick, 1984: 10). The large esophageal gland is also present in most members of the Cerithiidae (Houbrick, 1985:29) and

Modulidae (Houbrick, 1980:126). Litiopids, however, differ from members of the Cerithiidae in having a smooth mantle edge and in lacking a bipectinate osphradium. Bandel (1984:55), on the basis of radular configuration alone, erroneously placed *Alaba* close to *Cerithium*. However, a number of significant, apomorphic, anatomical characters separate litiopids from other cerithiacean families and define them as a unique group that should be given familial recognition. These include: 1) a median posterior, metapodial mucous gland that produces a strong mucus thread, anchoring the snail to its algal habitat [a mesopodial mucous gland also exists in the Turritellidae (Randles, 1900:57), but does not produce a mucus thread and is probably a convergence]; 2) location of the seminal receptacle in the lateral lamina of the pallial oviduct; 3) an extremely short, distal sperm gutter in the medial lamina of the pallial oviduct; 4) long, retractile epipodial tentacles along the sides and posterior of the foot; and 5) an unusual protoconch sculptured with numerous axial riblets and subsutural plaits. Other distinguishing characters are: 1) a very deep propodial cleft into which the anterior mucous gland empties; 2) extremely long, slender cephalic tentacles; 3) a long extensible, narrow foot; 4) an operculum with a narrow spiral ridge on the attached surface; 5) an hourglass-shaped rachidian tooth with a strong triangular buttress; 6) large, swollen albumen and capsule glands in the pallial oviduct; and 7) mound-shaped egg masses comprised of tightly coiled jelly ribbons.

The hypothesis that *Litiopa* and *Alaba* are closely related had been previously suggested by A. Adams (1862) and Robertson (1971). Anatomical, radular, and conchological evidence resulting from this study supports this hypothesis. The two genera are herein allocated to the family Litiopidae, as defined by the shared, derived characters described above.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. New York, 663 p., 24 pls.

Adams, A. 1860. On some new genera and species of Mollusca from Japan. Annals and Magazine of Natural History 6:331–337.

Adams, A. 1861. On some new genera and species of Mollusca from the north of China and Japan. Annals and Magazine of Natural History, series 3, 8:239–246.

Adams, A. 1862. On the animal and affinities of the genus *Alaba* with a review of the known species, and descriptions of some new species. Annals and Magazine of Natural History 1862:1–7.

Adams, H. and A. Adams. 1853–58. The genera of Recent Mollusca, 3 vols., 389 p., 138 pls.

Agassiz, J. L. R. 1846. Nomenclatoris Zoologici Index Universalis. Jent et Gassmann, Soloduri, 393 p.

Amio, M. 1963. A comparative embryology of marine gastropods, with ecological considerations. Journal of the Shimonosseki University of Fisheries 12(2–3):229–358.

Bandel, K. 1976. Observations on spawn, embryonic development and ecology of some Caribbean lower Mesogastropoda (Mollusca). The Veliger 18(3):249–271, 25 figs.

Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandelingen No. 214:188 p., 22 pls.

Cossmann, M. 1906. Essais de paléoconchologie comparée, vol. 7. Paris, 261 p., 14 pls.

Dall, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1887–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer 'Blake', Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. 29, Report on the Mollusca. Part 2, Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology 18:492 p., 40 pls.

Davis, G. M., V. Kitikoon, and P. Temcharoen. 1976. Monograph on "*Lithoglyphopsis*" *aperta*, the snail host of Mekong River schistosomiasis. Malacologia 15(2):241–287, 22 figs.

Fischer, P. 1880–87. Manuel de conchyliologie et de paléontologie conchyliologique. Paris, 1369 p., 23 pls., 1158 figs.

Franc, A. 1968. Classe des Gastéropodes (Gastropoda Cuvier, 1798). *In:* Grassé (ed.). Traité de zoologie, anatomie, systématique biologie, 5 (Mollusques Gastéropodes et Scaphopodes, III). Paris, 1083 p.

Grateloupe, J. P. S. de. 1828. Tableaux des coquilles fossiles qu'on recontre dans les terrains calcaires tertiares (faluns) des environs de Dax, dans le departement des Landes. Bulletin de la Societe Linneenne d'Histoire Naturelle, Bordeaux 2(9):72–109.

Habe, T. 1960. Egg masses and egg capsules of some Japanese marine prosobranchiate gastropod (sic). Bulletin of the Marine Biological Station of Asamushi 10(2):121–126, 11 figs.

Hedley, C. 1906. Studies on Australian Mollusca. Proceedings of the Linnean Society of New South Wales 30:522.

Hornung, A. and G. Mermoud. 1928. Mollusques de la Mer Rouge recueilles par A. Issel faisant partie des collections du Musée Civique d'Histoire Naturelle de Gênes. Cinquieme et derniere partie, Pleurotomides et Mitrides. Appendice. Litiopidés (p. 115–118). Annali del Museo Civico di Storia Naturale di Genova 53:108–121, 3 figs.

Houbrick, R. S. 1980. Review of the deep-sea genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae). Smithsonian Contributions to Zoology No. 321:30 p., 12 figs.

Houbrick, R. S. 1981. Anatomy of *Diastoma melanoides* (Reeve, 1849) with remarks on the systematic position of the family Diastomatidae (Prosobranchia: Gastropoda). Proceedings of the Biological Society of Washington 94(2): 598–621.

Houbrick, R. S. 1984. Revision of higher taxa in genus *Cerithidea* (Mesogastropoda: Potamididae) based on comparative morphology and biological data. American Malacological Bulletin 2:1–20, 5 figs.

Houbrick, R. S. 1985. Genus *Clypeomorus* Jousseaume (Cerithiidae: Prosobranchia). Smithsonian Contributions to Zoology No. 403:131 p., 62 figs.

Humason, G. L. 1962. Animal tissue techniques. San Francisco, 468 p.

Iredale, T. 1936. Australian molluscan notes. No. 2. Records of the Australian Museum 19:267–340, pls. 20–24

Iredale, T. 1955. Proceedings of the Royal Society of New South Wales 1953–54:81.

Iredale, T. and D. F. McMichael. 1962. A reference list of the marine Mollusca of New South Wales. The Australian Museum, Sydney, Memoir 11:109 p.

Keen, A. M. 1971. Sea shells of tropical West America, 2nd ed. Stanford University Press, Stanford, 1064 p., 22 pls.

Kilburn, R. N. and E. Rippey. 1982. Sea shells of southern Africa. Macmillan, Johannesburg, 249 p., 46 pls.

Kosuge, S. 1964. Anatomical study of *Diala goniochilia* (A. Adams) (Gastropoda). Bulletin of the National Science Museum 7(1):33–36, 10 figs.

Laseron, C. F. 1956. The families Rissoinidae and Rissoidae (Mollusca) from the Solanderian and Dampierian zoogeographical provinces. Australian Journal of Marine and Freshwater Research 7(3):384–487, 228 figs.

Lebour, M. V. 1945. The eggs and larvae of some prosobranchs from Bermuda. Proceedings of the Zoological Society of London 114:426–489.

Lesson, R. P. 1835. Illustrations de zoologie (20). Appendix, 14, no pagination.

Marcus, E. and E. Marcus. 1964. On *Cerithium atratum* (Born, 1778) (Gastropoda: Prosobranchia). Bulletin of Marine Science of the Gulf and Caribbean 14(3):494–510.

Melvill, J. C. 1904. Descriptions of twenty-three species of Gastropoda from the Persian Gulf, Gulf of Oman and Arabian Sea, dredged by Mr. F. W. Townsend of the Indo-European Telegraph Service, in 1903. Proceedings of the Malacological Society of London 6(1):51–60, 5 pls.; 158–169, pl. 10.

Nevill, G. 1885. Hand list of Mollusca in the Indian Museum, Calcutta. Part 2, Gastropoda. Prosobranchia-Neurobranchia (cont'd). Calcutta, 306 p.

Okutani, T., T. Habe, and K. Hasegawa. 1983. An observation on *Litiopa melanostoma*. Chiribotan 14(2):23–25.

Ponder, W. F. 1967. The classification of the Rissoidae and Orbitestellidae with descriptions of some new taxa. Transactions of the Royal Society of New Zealand 9(17):193–224, 13 pls.

Ponder, W. F. 1985. A review of the genera of Rissoidae (Mollusca: Mesogastropoda: Rissoacea). Records of the Australian Museum (1984), Supplement 4:221 p., 153 figs.

Randles, W. B. 1900. On the anatomy of *Turritella communis*, Risso. Proceedings of the Malacological Society of London 4:56–65, pl. 6.

Rang, P. S. 1829. Notice sur le Litiope, *Litiopa*, genre nouveau de Mollusques gasteropodes. Annales des Sciences Naturelles. 16(3):303–307.

Robertson, R. 1971. Scanning electron microscopy of planktonic larval marine gastropod shells. The Veliger 14(1):1–12, 9 pls.

Sacco, F. 1895. I Molluschi dei terreni Terziarii del Piemonte e della Liguria. Pt. 18 (Melaniidae, Littorinidae, Fossaridae, Rissoidae, Hydrobiidae, Paludinidae, e Valvatidae). Turin, 52 p., 1 pl.

Smith, E. A. 1875. Remarks on the genus *Alaba*, with the description of a new species. Proceedings of the Zoological Society of London 1875:537–540.

Thiele, J. 1929. Handbuch der Systematischen Weichtierkunde. Part 1. Jena, 376 p., 470 figs.

Tryon, G. W. 1882. Manual of conchology, first series, vol. 4:5–276, 58 pls. Philadelphia.

Wenz, W. 1938. Gastropoda, 1. *In:* Schindewolf. Handbuch der Paläozoologie 6(1):848 p., 2479 figs. Berlin.

Seasonal Recruitment of Marine Invertebrates to Hard Substrates on Georges Bank and the Eastern Continental Shelf of the United States

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ABSTRACT

Seasonal recruitment of marine invertebrates to hard substrates placed on the U.S. continental shelf from 1978 to 1981 was studied. A large fouling community was present at the bottom of Georges Bank and distinct patterns of settlement were observed for wood-boring pholads (*Xylophaga*), barnacles (*Chirona hameri*), and jingle shells (*Anomia squamula*). Seasonal changes in gonadal development of the pholads suggested late summer and late fall spawnings. Examination of wood samples from 85 stations helped to document the bathymetric and geographic distribution of nine species of pholads and eight species of teredinids on the U.S. continental shelf.

Key words: Recruitment; invertebrate larvae; hard substrates; wood panels; boring organisms; settlement; continental shelf; Georges Bank.

INTRODUCTION

This study was designed to examine patterns of seasonal recruitment of marine invertebrates to hard substrates on the continental shelf. It was conducted in conjunction with studies of sediment transport on the eastern United States continental shelf (Butman & Folger, 1979). Wood was chosen as the substrate so that organisms that live both in (wood-boring mollusks) and on hard substrates could be studied. Annual recruitment of animals with planktonic larvae could serve as a natural biological indicator of the effects of oil and gas drilling activities on the continental shelf.

MATERIALS AND METHODS

Settling panels of soft spruce (3.6 × 8.7 × 31.0 cm) were attached with plastic straps to bottom tripod systems designed to measure processes of bottom-sediment movement on the continental shelf (Butman & Folger, 1979). Samples were obtained from a total of 12 stations over a 3-year period (table 1; figures 1, 2). The bottom tripod systems measured water temperature, current, pressure, and light transmission, and photographed the seafloor every few hours (Butman & Folger, 1979). Panels were strapped to the tripods in a horizontal orientation approximately 1 m above the seafloor. Tripods were deployed for periods averaging 4 months duration (figure 2).

The entire panels were preserved in approximately 7% formalin seawater soon after the tripods were recovered. They were later examined under a dissecting microscope to determine species and number of individuals present, and to estimate the percent surface covered by each species. The presence of larvae or newly set juveniles was noted. Examples of each species were removed and stored in ethanol for identification. Wood borers were dissected from the panels, identified to species, and their shells removed. Tissues were embedded in paraffin, sectioned at 7 μm, stained with hematoxylin and eosin using standard histological procedures, and analyzed for gonadal ripeness.

Another set of samples of wood borers was obtained from the U.S. National Marine Fisheries Service (NMFS), which collected wood in its sampling gear during surveys of fisheries stocks on the continental shelf. Over a 5-year period (1976–81) a total of 142 pieces of wood was obtained from 85 stations, ranging from 34°N to 42°N at depths of 18 to 183 m (figure 1).

A third set of samples was received from a joint NMFS-USGS submarine cruise at 360 m on the continental slope near 39°03′N, 72°46′W (July, 1978). Wood borers dissected from all of these samples were treated identically to those obtained from the tripod panels.

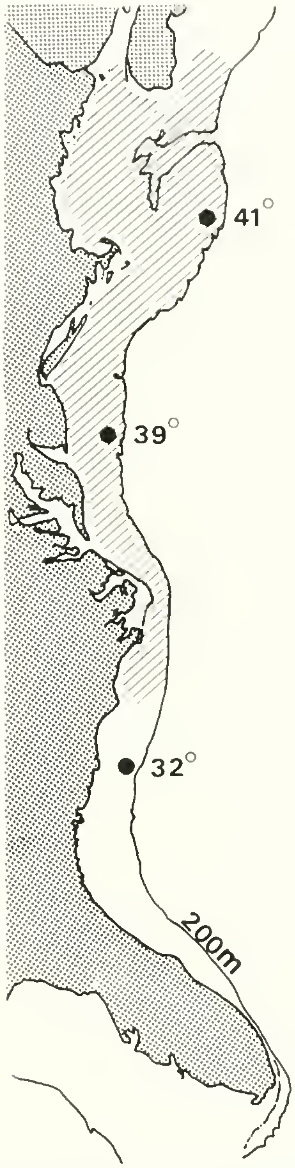

Figure 1. Eastern continental shelf of the United States with offshore 200-m contour line. Shading indicates area surveyed by the U.S. National Marine Fisheries Service during this study. Locations of the U.S. Geological Survey long-term monitoring stations are indicated by dots and their approximate latitudes. Exact locations of stations are given in table 1.

RESULTS

Georges Bank (Five Stations, 64 to 99 m)

The number and species of fouling organisms on each panel were dependent on a number of factors including recruitment, competition, predation, and succession. However, obvious patterns in colonization were observed over the 3-year (1978–82) sampling period. The most consistently present organisms on the wood panels were jingle shells (*Anomia squamula* Linné, 1758), barnacles (*Chirona hameri* Ascanius, 1767), and wood-boring pholads (*Xylophaga atlantica* Richards, 1942), but other species occurred as well (table 2). Greatest surface cover, nearly 90% at times, was provided by *A. squamula*, *C. hameri*, and the suite of hydroid species (table 2).

Table 1. Depth and location of monitoring stations.

Area	Station	Depth (m)	Latitude (N)	Longitude (W)
Georges Bank (41°)	A	85	40°51.2′	67°24.1′
	K	64	41°02.2′	67°33.5′
	P	71	40°29.0′	70°30.2′
	Q	67	40°29.9′	70°13.0′
	LCA	100	40°34.2′	67°44.8′
Mid-Atlantic (39°)	B	60	38°43.5′	73°36.5′
	D	41	38°58.9′	74°02.9′
	E	59	39°57.1′	72°35.6′
	F	234	38°31.0′	70°16.9′
Southern Atlantic (32°)	A	44	32°33.7′	78°39.5′
	B	47	31°06.8′	80°10.6′
	D	86	32°32.5′	78°37.5′

The timing of larval settlement was determined from the number and size of animals on the panels. The presence of larval forms or newly metamorphosed juveniles indicated that recruitment, but not necessarily spawning, had just occurred. The presence of large animals suggested that recruitment occurred during the early part of panel deployment, but because little is known of growth rates of invertebrates on the continental shelf, exact timing of recruitment could not be determined. Panels that were submerged for short periods (*e.g.*, a panel deployed for 26 days at Station P in October, 1978) provided better resolution of the timing of recruitment than panels deployed for the average 4-month

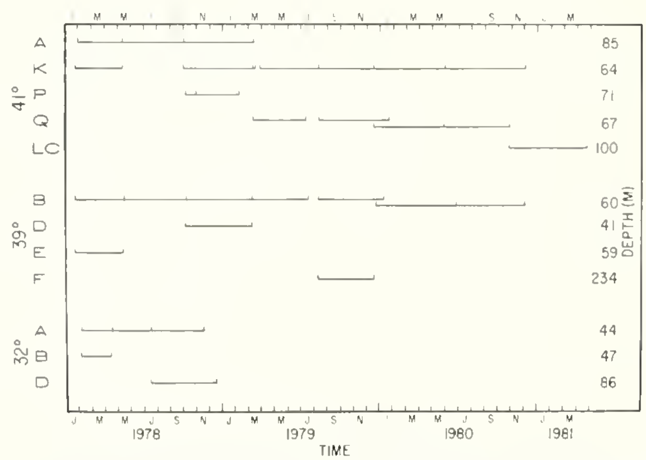

Figure 2. Sampling periods of U.S. Geological Survey tripods on the continental shelf of the eastern United States. Station locations are listed in table 1 and shown in figure 1.

Table 2. Fouling organisms present on wood panels from Georges Bank.

Cnidarians	Hydrozoans	*Tubularia crocea* (L. Agassiz, 1862)
		Tubularia couthouyi L. Agassiz, 1862
		Pennaria tiarella (Ayres, 1854)
		Clytia edwardsi (Nutting, 1901)
	Anthozoans	*Metridium senile* (Linné, 1758)
Annelids	Polychaetes	*Lepidonotus squamatus* (Linné, 1758)
		Antinoe sarsi (Kinberg, 1855)
Arthropods	Pycnogonids	*Callipallene brevirostris* (Johnson, 1837)
	Cirrepedia	*Chirona hameri* (Ascanius, 1767)
	Amphipods	*Gammarus annulatus* Smith, 1874
	Caprellids	*Aeginina longicornis* (Kroyer, 1843)
Mollusks	Eolids	*Eubranchus pallidus* (Alder and Hancock, 1842)
	Bivalves	*Anomia squamula* Linné, 1758
		Xylophaga atlantica Richards, 1942
		X. species 1, 2, 3, 4 (Turner, ms.)
		Placopecten magellanicus (Gmelin, 1791)
Ectoprocts		*Microporella ciliata* (Pallas, 1766)
		Barentsia laxa Kirkpatrick, 1890

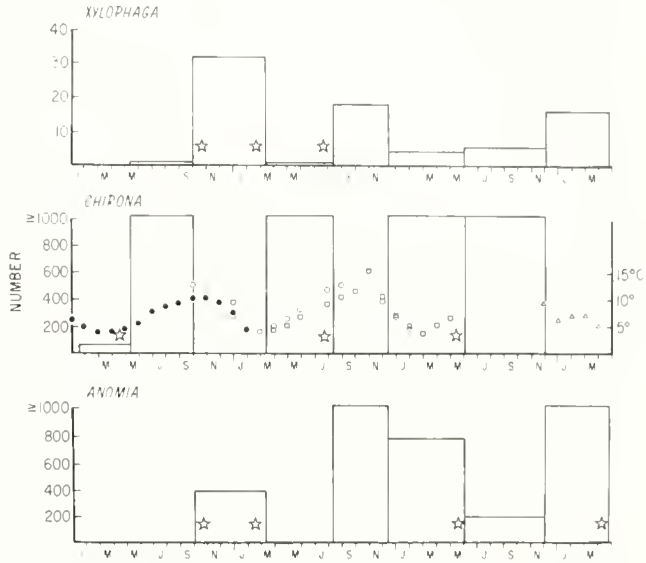

Figure 3. Mean seasonal abundance of *Anomia squamula*, *Chirona hameri*, and *Xylophaga atlantica* on fouling panels recovered from the Georges Bank. Stars indicate periods of settlement as determined by the presence of newly settled animals on the panels.
The mean monthly bottom-water temperatures measured by the tripod systems are shown in the middle graph. Temperatures indicated by solid dots (●) are from Station A, circles (○) from Station K, open squares (□) from Station Q, and open triangles (△) from Station LC. For a more detailed description of the seasonal cycle of temperature at Station A on Georges Bank, see Butman and Beardsley (in press).

period. Finally, because the timing of deployment varied slightly each year, different periods were sampled. Interpretation of the data was difficult, but the repeatability of distinct periods of settlement during the 3 years of the study sampled is remarkable (figure 3).

Newly set larvae of *Anomia squamula* occurred on panels recovered in October and March; animals with shells less than 2 mm occurred on panels recovered in April and the beginning of June. Large numbers of animals settled on the panels deployed from October to May, with little or no recruitment during the summer months.

Chirona hameri cyprid larvae and newly metamorphosed juveniles were collected in May, June, and August, suggesting spring and summer recruitment. Panels deployed during fall and winter were notably free of barnacles.

Xylophaga atlantica larvae or juveniles less than 1 mm in shell length were collected in October, December, early March, and August. Panels deployed in the spring, during periods of coldest bottom-water temperatures on the Georges Bank (figure 3), had the least amount of recruitment. This same pattern was observed for the scallop *Placopecten magellanicus* Gmelin, 1791, which was collected only from October to mid-March and again from August to January.

Mid-Atlantic Region (45 Stations, 41 to 234 m)

The single panel submerged at the shallow-water station on the Middle Atlantic Bight (41 m) from October, 1978 to March, 1979 was covered with hydroids and mud tubes. Fifty-nine specimens of *Xylopholas altenae* Turner, 1972 less than 1.56 mm in shell length and a few large *Anomia squamula* (8.5 mm) were also removed. At intermediate-depth stations (59 and 66 m), hydroids were present May through December. Based upon the presence of newly set juveniles, it appears that *Anomia squamula* set only during that period as well. Very small numbers of recently metamorphosed *X. atlantica* were found throughout the year in every panel, with the exception of a single panel submerged May through October, 1978 when water temperatures were at a low of 5 to 9 °C. Panels submerged in subsequent years overlapped this period and showed settlement. At the deep station (234 m) the only fouling organism was *X. atlantica*. Both large and newly metamorphosed specimens

Table 3. Wood-boring mollusks collected during this study along the continental shelf of the eastern United States. Asterisk (*) indicates range extensions.

Pholadidae	Teredinidae
Xylophaga atlantica Richards, 1942	*Teredo navalis* Linné, 1758
Jouannetia quillingi Turner, 1955*	*Bankia gouldi* (Bartsch, 1908)
Xylopholas altenae Turner, 1972*	*Bankia carinata* (Gray, 1827)
Martesia fragilis Verrill and Bush, 1890	*Lyrodus floridanus* (Bartsch, 1908)
Barnea truncata (Say, 1822)	*Nototeredo knoxi* (Bartsch, 1917)
Xylophaga species 1. Turner, ms.	*Psiloteredo megotara* Hanley, 1848
Xylophaga species 2. Turner, ms.	*Teredothyra matocotana* (Bartsch, 1927)
Xylophaga species 3. Turner, ms.	*Teredora malleolus* (Turton, 1822)
Xylophaga species 4. Turner, ms.*	

were removed from the panel, indicating settlement throughout the period of submergence.

Southern Atlantic Region (Three Stations, 44 to 86 m)

Tripods were deployed in the South Atlantic Bight over an 11-month period in 1978. Recruitment at mid-shelf depths (44 and 47 m) was distinctly different from recruitment at the 86-m station. At the shallow stations the wood borers of *Xylophaga* (Turner species 4) and *Bankia carinata* (Gray, 1827) (table 3) bored into the panels from April through mid-July when water temperatures were approximately 19 °C. No wood borers appeared from mid-July through November. Barnacles, *Balanus amphitrite* (Linné, 1767) and *B. venustus* (Linné, 1767), and the bivalves *Hiatella arctica* (Linné, 1767) and *Chione cancellata* (Linné, 1767) settled during February to mid-April. From mid-April to July the panel was covered with hydroids and barnacles. These were also present from July to November, with additional settlement of *C. cancellata* and the serpulid worm *Serpula vermicularis* (Linné, 1767). A panel placed at the deep station near the edge of the shelf (86 m) from July to December had little surface fouling, but was infested with large wood borers (*Xylophaga* species 4), *Teredothyra matacatona* (Bartsch, 1927), and *Bankia gouldi* (Bartsch, 1908) (table 3). Water temperatures

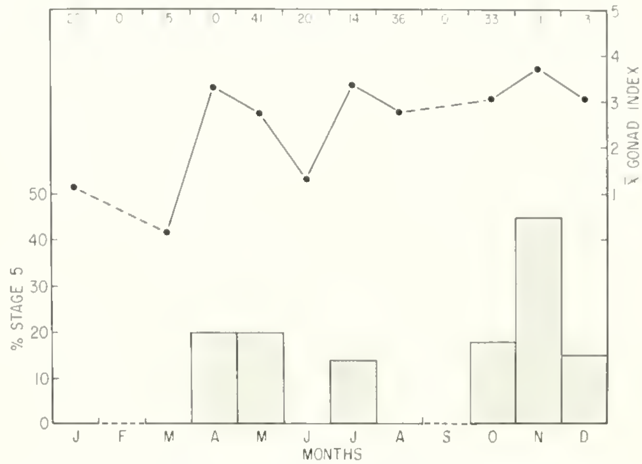

Figure 4. Percent of population of *Xylophaga* species with gonads in stage 5 ripe condition and mean gonad index for the months the animals were collected. Monthly sample size is given at the top of the graph.

reached mean monthly values of 18.9 °C for July and a high of 24.4 °C for November.

Wood-Boring Mollusks

From the total collection of wood samples provided by the tripod deployments and by the U.S. National Marine Fisheries Service, nine species of pholads (Pholadidae) and eight species of shipworms (Teredinidae) were identified (table 3). *Xylophaga atlantica* was found only north of Cape Hatteras and was the most common pholad in northern areas. It was collected at depths of 42 to 234 m, but only settled on panels at stations deeper than 60 m on the Middle Atlantic Bight and on Georges Bank. An undescribed species of *Xylophaga* (Turner species 4) settled only at the South Atlantic Bight stations. Its distribution overlapped little with *X. atlantica*. *Xylopholas altenae*, previously known from a few deep stations off Florida (Turner, 1972a), was collected at both shallow (41 m) and deep (360 m) USGS stations at 39°N, firmly establishing this northern range extension. Only single samples of the other pholads were collected.

Histological examination of the gonads of the pholads indicated gonadal ripening during the spring and spawning during summer and late fall (figure 4) when bottom water temperatures exceeded 10 °C on the Georges Bank. With a long planktonic stage predicted (Culliney & Turner, 1976), the larvae would not be expected to settle and metamorphose until the fall and winter.

Table 4. *Anomia* size analysis from buoy data of Merrill (1962) and Merrill and Edwards (1976).

Buoy	*Nantucket Lightship* Buoy	*4 Davis Shoals* #1 Buoy	*4 Davis Shoals* #2 Buoy
Location	40°33′N, 69°28′W	40°57′N, 69°55′W	40°57′N, 69°55′W
Dates in field	10/8/57–5/10/58	5/7/57–5/15/58	5/15/58–11/10/58
Mean size (mm) of *Anomia*	$\bar{x} = 4.7$	$\bar{x} = 9.1$	$\bar{x} = 2.4$

DISCUSSION

The observed seasonal settlement of the key species (*Anomia squamula*, *Chirona hameri*, and *Xylophaga atlantica*) is quite striking. There are only a few studies in the literature that discuss seasonal settlement of these organisms.

Seasonality of occurrence of *Anomia squamala* has been reported. Lebour (1938) found *A. squamula* larvae common in the plankton throughout the year off England, but especially in early autumn. Jorgensen (1946) stated that *A. squamula* spawn from July to September off Denmark, but larvae were also noted in November and December. Dons (1936; *in* Jørgensen, 1946) reports attachment of young to occur only during 3 months in southern Norway, with a peak in either August or September. Merrill (1962) and Merrill and Edwards (1976) studied *A. squamula* settlement on surface buoys just south of Georges Bank and found heavy settlement in the autumn (table 4), as reported in this study. It appears, therefore, that throughout its distribution in northern latitudes, *A. squamula* has greatest recruitment during autumn and winter. Off New England, settlement occurs both at the surface and at the bottom during this time. Insufficient data are provided in the earlier papers to correlate settlement with environmental factors such as water temperature.

We could find no reference to seasonality of spawning and settlement of *C. hameri*, nor to other species of barnacles on Georges Bank. Based on the data presented here, settlement of *C. hameri* at the bottom on Georges Bank appears restricted to a short period from late April through July.

Almost nothing is known about the life history and reproductive biology of species of *Xylophaga*. Short-term placement of panels has shown that settlement of *X. dorsalis* occurs between December and April off Millport, Scotland (Turner & Johnson, 1971), and that settlement of *X. washingtona* occurs between November and January off Oregon (Turner and Johnson, 1971) and year-round in California (Haderlie, 1983). Although *X. atlantica* has been reared to metamorphosis (Culliney & Turner, 1976) little else is known concerning its reproductive or general biology. Our work suggests spawning occurs in summer and again in late fall for these pholads. On Georges Bank, *X. atlantica* metamorphoses and bores into wood primarily between September and February. At the Mid-Atlantic site this occurs 2 months later (November through April) and again later at the Southern Atlantic site (December through June). This reflects differences in periods of peak water temperatures at these three areas.

Turner (1955) reviewed the available information on pholads and emphasized how little was known. Purchon (1941) discussed the biology of *X. dorsalis*, including descriptions of general anatomy and feeding. Tipper (1968) was the first to study the ecology of deep-sea wood borers. He found *X. washingtona* in panels set at depths of 200, 500, and 1,000 m on the continental terrace off Oregon. In general, the number of *X. washingtona* per square centimeter decreased with increasing depth, and increased over time. The teredinid *Bankia setacea* was also present in his collecting panels set at 200 m, but he did not recover them from shallower depths, and attributed this to seasonal patterns of reproduction and coastal upwelling. Haderlie (1983) found the overlap in *B. setacea* and *X. washingtona* to occur only between 35 and 70 m in Monterey Bay, California. Below that, *X. washingtona* was the only wood borer present and settled during all months of the year. Water temperatures at 70 m averaged 10 °C and were only slightly colder at deeper sites.

DePalma (1963), in a series of tests conducted off Florida, also documented an overlap in bathymetric ranges of teredinids (*Bankia carinata*) and pholads (*Xylophaga* sp.). *Bankia carinata* was found in test panels set as deep as 165 m, but only in low numbers. Pholads were common in panels set at 90 m, but none were found at depths less than 30 m (Turner, 1966). In recent tests, DePalma obtained *Teredothyra matacotana* in wood set at 200 m, making this the deepest record for teredinids invading new wood (Turner, personal observation). However, pholads invade the depths of the oceans (Turner, 1972a,b, 1973a,b, 1981).

In the northwestern Atlantic, *Teredo navalis* and *Xylophaga atlantica* exhibit overlapping bathymetric ranges, with *T. navalis* extending from intertidal down to 66 m and *X. atlantica* from 18 m (Turner & Johnson, 1971) to 234 m. In our study two minute teredinids were collected with *X. atlantica* in a panel at 67 m on Georges Bank and one *T. navalis* was collected among the *X. atlantica* at 60 m on Mid-Atlantic Station B. In the South Atlantic Bight *Xylophaga* (Turner species 4) occurred with *Bankia carinata* at 44 m and with *Teredothyra matacotana* and *Bankia gouldi* at 86 m. These panels were carried quickly to the bottom, and so could not have become infested on the way down. Consequently, the reported occurrence of these borers indicates their true bathymetric range. Wood collected from the bottom by the National Marine Fisheries Service was probably infested with teredinids at the surface or while slowly sinking from the surface, and cannot be used to describe bathymetric distributions.

Some planktonic larvae of marine invertebrates live in the water column for extended periods of time before they settle to the bottom and metamorphose into juvenile benthic forms. During their planktonic stage they serve as food for other pelagic organisms, especially fish. Alteration of the marine environment by outer continental shelf exploratory drilling and production might have long-term effects upon phytoplankton production, zooplankton production (including larvae), and fish production. The use of wood panels to measure recruitment might be used to measure some of these perturbations, although the variability observed in this study and the difficulty in separating larval availability and observed recruitment suggests that interpretation of such simple monitoring studies would be difficult. Seasonal patterns

of larval recruitment might be better defined and correlated to physical parameters (water temperature, currents, *etc.*) if panels were deployed for short periods in overlapping succession.

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LITERATURE CITED

Butman, B. and R. C. Beardsley. In press. Long-term observations on the southern flank of Georges Bank; Part I. Seasonal cycle of current, temperature, stratification and wind stress. Journal of Physical Oceanography.

Butman, B. and D. W. Folger. 1979. An instrument system for long-term sediment transport studies on the continental shelf. Journal of Geophysical Research 84:1215–1220.

Culliney, J. L. and R. D. Turner. 1976. Larval development of the deep-water wood boring bivalve, *Xylophaga atlantica* Richards (Mollusca, Bivalvia, Pholadidae). Ophelia 15: 149–161.

DePalma, J. R. 1963. Marine boring and fouling organisms off Fort Lauderdale, Florida. U.S. Naval Oceanographic Office. Marine Sciences Department, Informal Manuscript No. 0-70-62a, 27 p.

Haderlie, E. C. 1983. Depth distribution and settlement times of the molluscan wood borers *Bankia setacea* (Tryon, 1863) and *Xylophaga washingtona* Bartsch, 1921, in Monterey Bay. The Veliger 25:339–342, 2 pls.

Jørgensen, C. B. 1946. Lamellibranchia. Meddelelser Kommissionen Danmarks Fiskeri- og Havundersøgelser, Serie Plankton 4:277–311.

Lebour, M. V. 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae. Journal of the Marine Biological Association of the United Kingdom 23: 119–144.

Merrill, A. S. 1962. Variation and change in surface sculpture in *Anomia aculeata*. The Nautilus 75:131–138.

Merrill, A. S. and R. L. Edwards. 1976. Observations on mollusks from a navigation buoy with special emphasis on the sea scallop *Placopecten magellanicus*. The Nautilus 90:54–61.

Purchon, R. D. 1941. On the biology and relationships of the lamellibranch *Xylophaga dorsalis* (Turton). Journal of the Marine Biological Association of the United Kingdom 25: 1–39.

Tipper, R. C. 1968. Ecological aspects of two wood-boring molluscs from the continental terrace off Oregon. Doctoral dissertation, Oregon State University, Corvallis, OR, 137 p.

Turner, R. D. 1955. The family Pholadidae in the western Atlantic and the eastern Pacific. Part II—Martesiinae, Jouannetiinae, and Xylophaginae. Johnsonia 3:65–160, pls. 35–93.

Turner, R. D. 1966. Implications of recent research in the Teredinidae. Beihefte zu Material und Organismen, Berlin, Heft 1:437–446.

Turner, R. D. 1972a. A new genus and species of deep-water wood-boring bivalves (Mollusca, Pholadidae, Xylophagainae). Basteria 36:97–104.

Turner, R. D. 1972b. *Xyloredo*, a new teredinid-like abyssal wood-borer (Mollusca, Pholadidae, Xylophagainae). Breviora 397:1–19, pls. 1–6.

Turner, R. D. 1973a. Deep water wood-boring mollusks. Proceedings of the Third International Congress on Marine Corrosion and Fouling, National Bureau of Standards, Gaithersburg, Maryland, p. 836–841.

Turner, R. D. 1973b. Wood-boring bivalves, opportunistic species in the deep sea. Science 180:1377–1379.

Turner, R. D. 1981. "Wood islands" and "thermal vents" as centers of diverse communities in the deep sea. Biologiya Morya 1:3–10.

Turner, R. D. and A. C. Johnson. 1971. Biology of wood-boring molluscs. *In:* Jones, E. B. G. and S. K. Eltringham (eds.). Marine borers, fungi and fouling organisms of wood. Organisation for Economic Co-operation and Development, Paris, p. 259–301.

North American Hydrobiidae (Gastropoda: Rissoacea): Redescription and Systematic Relationships of *Tryonia* Stimpson, 1865 and *Pyrgulopsis* Call and Pilsbry, 1886

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ABSTRACT

Anatomical details are provided for the type species of *Tryonia* Stimpson, 1865, *Pyrgulopsis* Call and Pilsbry, 1886, *Fontelicella* Gregg and Taylor, 1965, and *Microamnicola* Gregg and Taylor, 1965, in an effort to resolve the systematic relationships of these taxa, which represent most of the generic-level groups of Hydrobiidae in southwestern North America. Based on these and other data presented either herein or in the literature, *Hyalopyrgus* Thompson, 1968 is assigned to *Tryonia*; and *Fontelicella*, *Microamnicola*, *Natricola* Gregg and Taylor, 1965, *Marstonia* F. C. Baker, 1926, and *Mexistiobia* Hershler, 1985 are allocated to *Pyrgulopsis*.

The ranges of both *Tryonia* and *Pyrgulopsis* include parts of eastern and western America and northern Mexico. *Tryonia* is closely related to a group of North and Central American littoridinine genera having an elongate-conic shell and (mammiform) glandular penial lobes, and *Pyrgulopsis* (Nymphophilinae) is closely allied to *Cincinnatia* Pilsbry, 1891 from eastern North America.

INTRODUCTION

Prosobranch snails of the family Hydrobiidae comprise a major faunal element of North American freshwaters, numbering some 28 genera and 148 species (Burch, 1982). Despite their diversity and ubiquity, North American Hydrobiidae are poorly understood in terms of systematics, as the anatomy of few species is known. While recent advances have been made in the systematic study of southeastern Hydrobiidae (Thompson, 1968, 1969, 1977, 1984; Thompson & McCaleb, 1978), the fauna of other large expanses of territory is virtually unstudied.

One such fauna is that of the arid Southwest. Of the generic-group taxa found in this region, only *Fluminicola* Stimpson, 1865 has received sufficient morphological study to allow clarification of its relationships (Thompson, 1984). Relatively little is known of *Pyrgulopsis* Call and Pilsbry, 1886, *Tryonia* Stimpson, 1865, and *Fontelicella* Gregg and Taylor, 1965, the latter two of which comprise more than 30 species (mostly undescribed) in the Southwest. Taylor (1966) placed *Tryonia* in the Littoridininae Taylor, 1966 on the basis of its turreted shell and glandular penial lobes. It is clear from the initial descriptions and subsequent studies illustrating the penis (Russell, 1971: fig. 4; Taylor, 1983:16–25) that *Fontelicella* and its subgenera, *Natricola* Gregg and Taylor, 1965 and *Microamnicola* Gregg and Taylor, 1965 belong to the Nymphophilinae Taylor, 1966 (see Thompson, 1979). While the type species of *Pyrgulopsis*, *P. nevadensis* (Stearns, 1883), has not received anatomical study, the penes of several eastern species have been examined by Thompson (1977), who suggested that the genus may be a nymphophiline. The scant published morphological data do not, however, allow meaningful comparisons of the above with other Hydrobiidae.

Our anatomical study of the type species of *Tryonia* and *Hyalopyrgus* Thompson, 1968 showed that *Hyalopyrgus*, endemic to Florida (and placed in the Littoridininae by Davis *et al.*, 1982), should be allocated to *Tryonia*. Similarly, study of type species and published accounts indicated that *Fontelicella*, *Natricola*, *Microamnicola*, as well as *Mexistiobia* Hershler, 1985 (from northern Mexico) and *Marstonia* F. C. Baker, 1926 (widespread in eastern North America) should be allocated to *Pyrgulopsis*. In this paper we redescribe *Tryonia* and *Pyrgulopsis* and briefly discuss their affinities.

MATERIALS AND METHODS

Anatomical illustrations given in this paper are based on study of the following lots (representing fully relaxed alcohol material unless otherwise indicated): *Tryonia clathrata* Stimpson, 1865, Moapa Springs, Clark County, NV, USA, USNM 850291; *Hyalopyrgus aequicostatus* (Pilsbry, 1889), Lake Dora, Lake County, FL, USA, USNM 847212; Alexander Springs, Lake County, FL, USA, UF uncatalogued lot; *Pyrgulopsis nevadensis*, rehydrated (in Bouin's solution) bodies, south end of Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot; *Pyrgulopsis archimedis* S. S. Berry, 1947, unrelaxed, Upper Klamath Lake, Klamath County, OR,

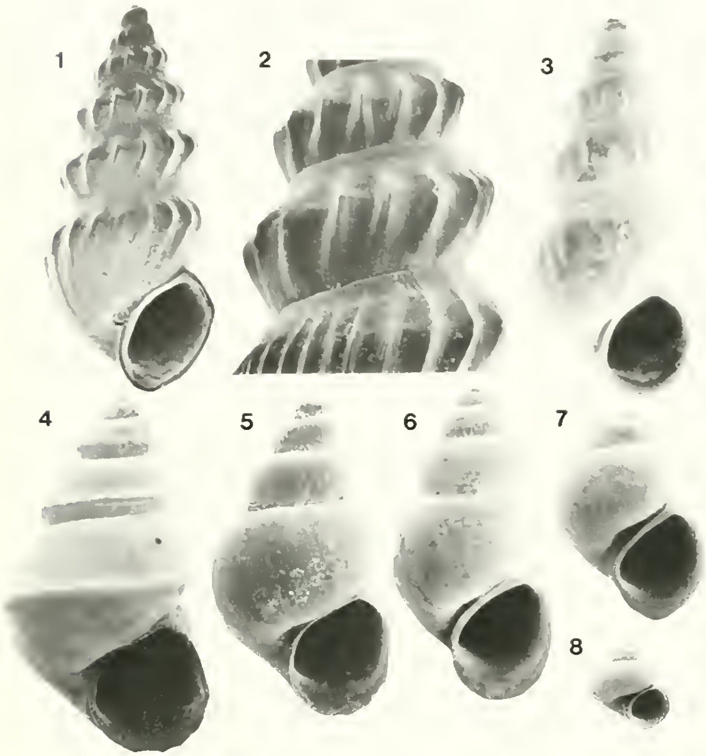

Figure 1. Photograph (SEM) of holotype of *Tryonia clathrata* Stimpson, Colorado Desert, CA, USA (but see Taylor, 1966: 197), ANSP 27969. Shell height is 4.36 mm. **Figure 2.** Close-up photograph of shell of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, showing sculptural pattern. The height of the portion of shell photographed is 2.36 mm. **Figure 3.** Photograph of shell of *Tryonia aequicostata* (Pilsbry), Lake Dora, Lake County, FL, USA, USNM 847212, printed to same enlargement as figure 1. **Figure 4.** Photograph of paratype of *Pyrgulopsis nevadensis*, south end of Pyramid Lake, Washoe County, NV, USA, USNM 75450, printed to same enlargement as figure 1. **Figure 5.** Photograph of shell of *Pyrgulopsis lustrica* (Pilsbry), Little Lakes, Herkimer County, NY, USA, USNM 28085, printed to same enlargement as figure 1. **Figure 6.** Photograph of paratype of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292, printed to same enlargement as figure 1. **Figure 7.** Photograph of shell of *Pyrgulopsis micrococcus* (Pilsbry), Springdale Springs, Nye County, NV, USA, USNM 850297, printed to same enlargement as figure 1. **Figure 8.** Photograph of shell of *Pyrgulopsis manantiali* (Hershler), spring at Tierra Blanca, SW of Cuatro Cienegas, Coahuila, MEX, ANSP A9888L, printed to same enlargement as figure 1.

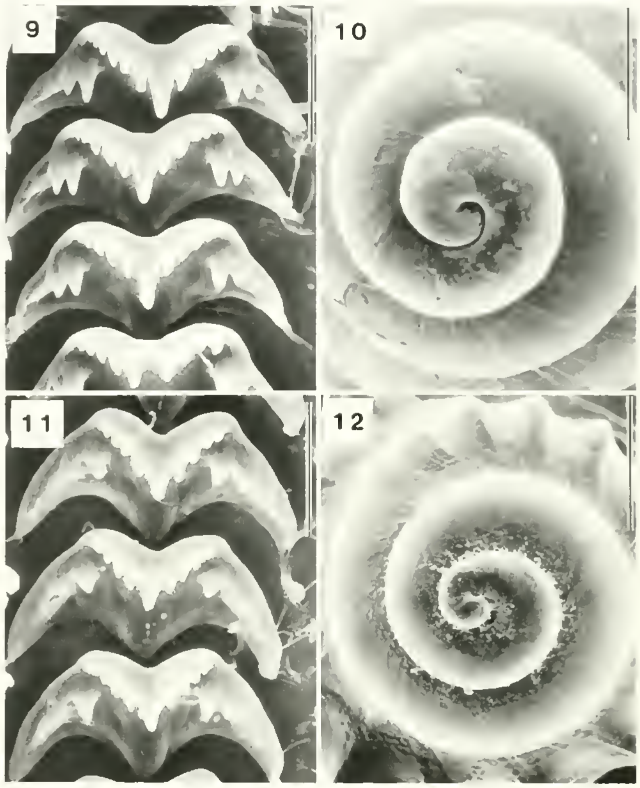

Figure 9. Photograph (SEM) of central radular teeth of *Tryonia aequicostata* (Pilsbry), Lake Dora, Lake County, FL, USA, USNM 847212. Scale bar equals 10 μm. **Figure 10.** Photograph of protoconch of *Tryonia aequicostata* (Pilsbry) (from same lot as above). Scale bar equals 150 μm. **Figure 11.** Photograph of central radular teeth of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291. Scale bar equals 10 μm. **Figure 12.** Photograph of protoconch of *Tryonia clathrata* Stimpson (from same lot as above). Scale bar equals 150 μm.

USA, ANSP A602b; *Pyrgulopsis letsoni* (Walker, 1901), creek W of Crenshaw Lake, Oakland County, MI, USA, UF 91726; *Pyrgulopsis scalariformis* (Wolf, 1869), Meramec River, 12.0 km SE of Leesburg, Crawford County, MO, USA, UF 91727. *Fontelicella (sensu stricto) californiensis* Gregg and Taylor, 1965, Campo Creek, San Diego County, CA, USA, USNM 850292 (paratypes); *Fontelicella (Microamnicola) micrococcus* (Pilsbry *in* Stearns, 1893), Springdale Springs, Nye County, NV, USA, USNM 850297; *Mexistiobia manantiali* Hershler, 1985, small spring at Tierra Blanca, SW of Cuatro Cienegas, Coahuila, MEX, ANSP A98881.

Snails were dissected in dilute Bouin's solution at 50× using a Wild M-8 dissecting microscope. Ciliation patterns on the cephalic tentacles and penis were examined using a Hitachi S-570 scanning electron microscope, with the animals having first been graded into 100% ETOH and dried using a Denton DCP-1 Critical Point Drier. Shells and radulae were cleaned with Clorox and then photographed using the scanning electron microscope.

SYSTEMATICS

Genus *Tryonia* Stimpson, 1865

Tryonia Stimpson, 1865:54. Type species: *Tryonia clathrata* Stimpson, 1865:54, by original designation; 1865:54.

Hyalopyrgus Thompson, 1968:43. Type species: *Bythinella aequicostata* Pilsbry, 1889:86, by original designation; Thompson, 1968:45.

Diagnosis: Shell (figures 1–3) colorless, transparent, elongate-conic to turreted, 1.7–7.0 mm tall with 4.0–8.0

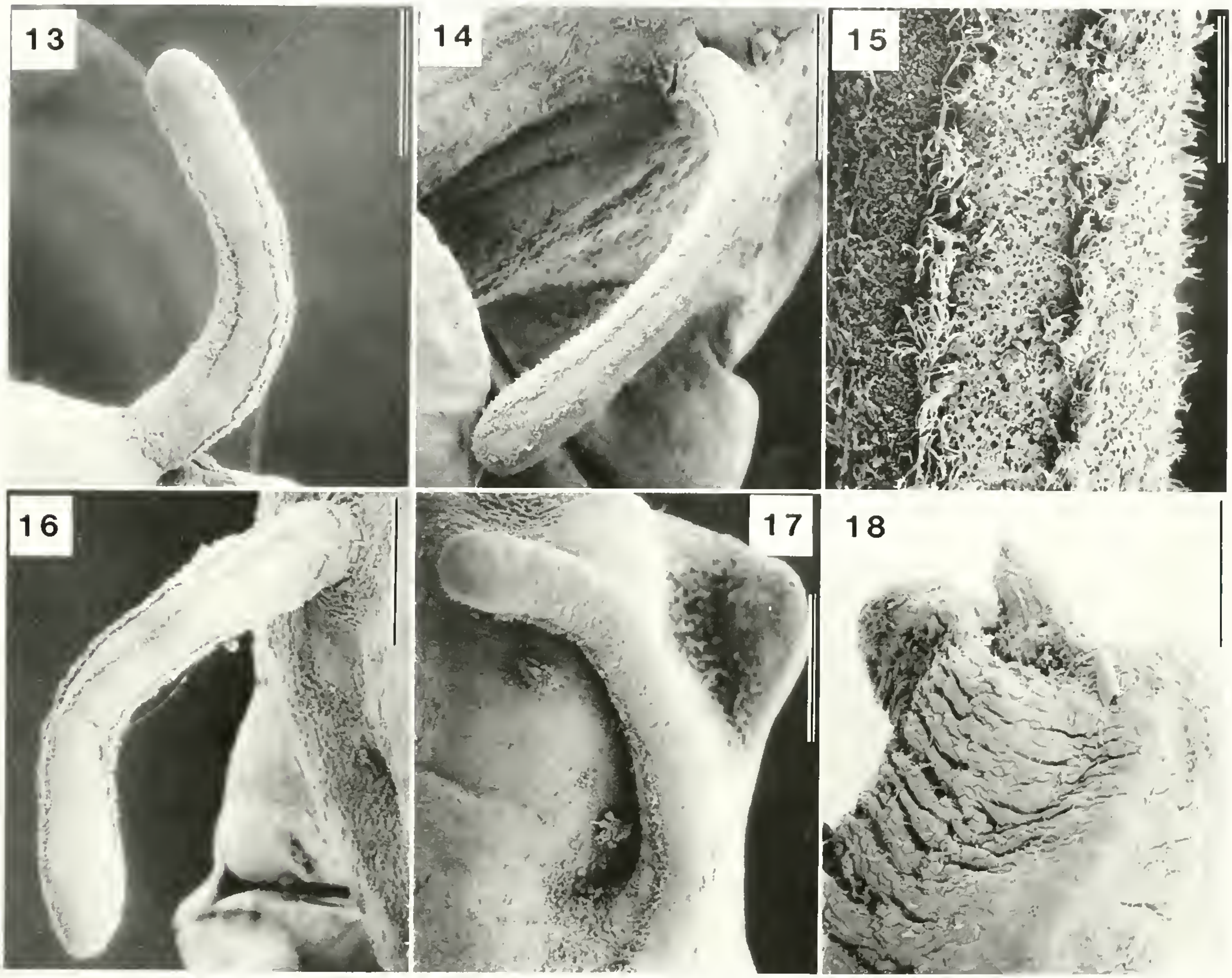

Figure 13. Photograph (SEM) of left tentacle of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, showing ciliary tracts. Scale bar equals 176 μm. **Figure 14.** Photograph of right tentacle of *Tryonia clathrata* Stimpson (from same lot as above). Scale bar equals 170 μm. **Figure 15.** Close-up photograph of ciliary tracts on right tentacle of *Tryonia clathrata* Stimpson (same specimen as above). Scale bar equals 30 μm. **Figure 16.** Photograph of left tentacle of *Tryonia aequicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. Scale bar equals 176 μm. **Figure 17.** Photograph of right tentacle of *Tryonia aequicostata* (Pilsbry) (from same lot as above). Scale bar equals 200 μm. **Figure 18.** Photograph of penial tip of *Tryonia clathrata*, Moapa Springs, Clark County, NEV, USA, USNM 850291, showing sparse ciliation, terminal papilla, and blunt swelling on inner (left) side. Scale bar equals 50 μm.

whorls; typically high-spired with rounded whorls and indented sutures. Aperture simple, unthickened, and complete. Umbilicus narrow or absent. Sexual dimorphism pronounced, with males often half of female shell height. Protoconch (figures 10, 12) flat or slightly protruding, smooth or slightly wrinkled. Teleoconch sculpture consisting of fine growth lines, sometimes coupled with weak spiral lines or collabral striations or varices. Central tooth of radula (figures 9, 11) broader than tall, with 1–3 pairs of basal cusps. Digestive gland without anterior lobe. Cephalic tentacles with several elongate ciliary tracts (figures 13–17). Flattened penis (figures 19, 20) elongate and slender, with a single, enlarged glandular (mammiform) lobe at its base and 1–4 smaller glandular lobes on the inner curvature. Distal portion of penis ciliated (figure 18) to varying degrees, base sometimes also ciliated. Tip of penis with blunt swelling on inner curvature. Females ovoviviparous, with 3–15 embryos brooded in enlarged capsule gland (figure 21). Capsule gland with muscular sphincter at anterior end. Pallial oviduct reflected posteriorly, albumen gland reduced in size (figure 22, Ag). Small-sized bursa copulatrix and seminal receptacle ventral to albumen gland; coiled seminal receptacle duct opens into short spermathecal duct (figures 23, 24, Osr).

Species included: *Bythinella aequicostata*; *Bythinella brevissima* Pilsbry, 1890:64; *Potamopyrgus cheatumi*

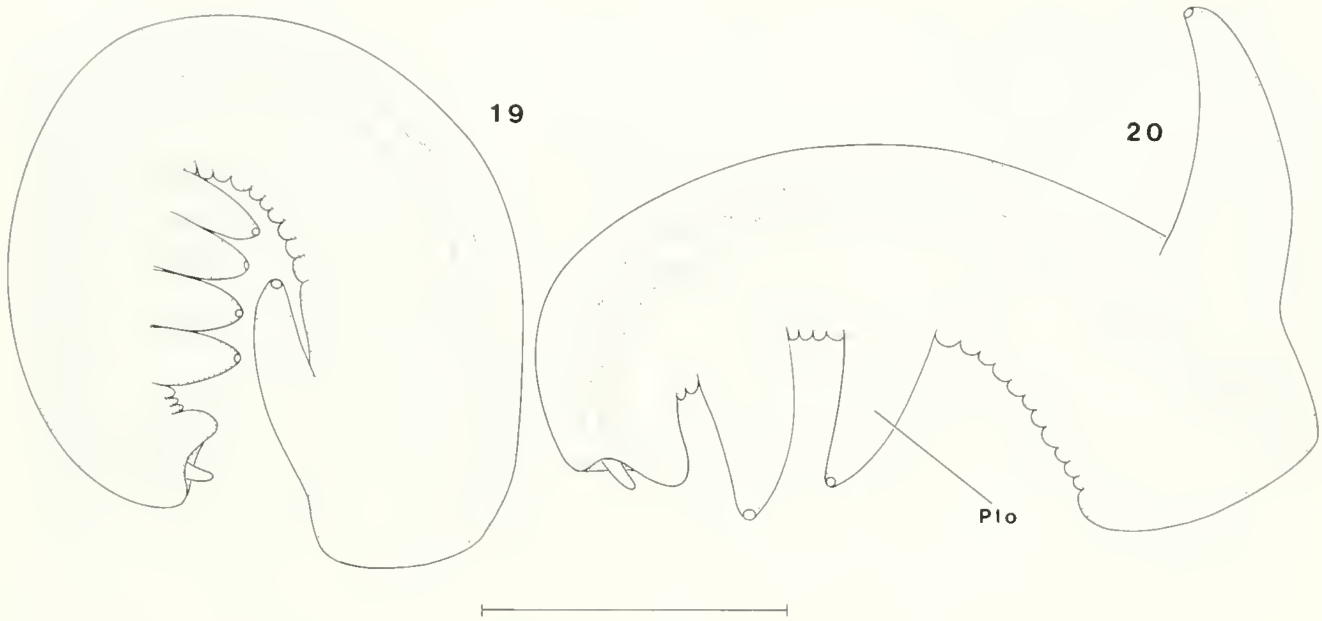

Figure 19. Penis of *Tryonia clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291. **Figure 20.** Penis of *Tryonia aequicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. Patterns of ciliation are not shown. Plo = penial lobe.

Pilsbry, 1935:91; *Calipyrgula circumstriata* Leonard and Ho, 1960a:125; *Tryonia clathrata*; *Paludestrina diaboli* Pilsbry and Ferriss, 1906:125; *Paludestrina imitator* Pilsbry, 1899:121; *Calipyrgula pecosensis* Leonard and Ho, 1960b:110; *Amnicola protea* Gould, 1855:129; *Paludestrina stokesi* Arnold, 1903:22.

The identity of the Central and South American taxa assigned to *Tryonia* by Taylor (1966) is uncertain due to lack of anatomical study.

Distribution: *Tryonia* occurs in much of Florida as well as in the arid Southwest, including parts of California, Nevada, Arizona, New Mexico, and Texas, and northern Mexico.

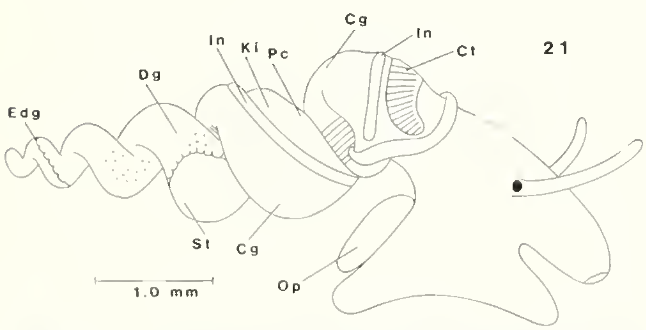

Figure 21. *Tryonia clathrata* Stimpson (without shell), Moapa Springs, Clark County, NV, USA, USNM 850291, viewed from the right side. Note the enlarged capsule gland (Cg) with embryos (dotted circles). The thickened dots on the digestive gland (Dg) are pigment granules. Cg = capsule gland, Ct = ctenidium, Dg = digestive gland, Edg = posterior end of digestive gland, In = intestine, Ki = kidney, Op = operculum, Pc = pericardium, St = stomach.

Remarks: Given the overall similarity between the Floridian and southwestern species, even extending to details of the bursa copulatrix complex (figures 23, 24), there can be no doubt that these species belong to a single genus. *Tryonia* belongs to a group of littoridinines having an elongate-conic shell and mammiform glandular lobes on the penis that includes *Aphaostracan* Thompson, 1968, *Littoridinops* Pilsbry, 1952, *Mexipyrgus* Taylor, 1966, and *Pyrgophorus* Ancey, 1888 (but not *Durangonella* Morrison, 1945; contrary to Hershler, 1985). *Tryonia* is distinguished from the above by its turreted shell and unique position of its penial lobes.

Genus *Pyrgulopsis* Call and Pilsbry, 1886

Pyrgulopsis Call and Pilsbry, 1886:9. Type species: *Pyrgula nevadensis* Stearns, 1883:173, by original designation; Call and Pilsbry, 1886:9.

Marstonia F. C. Baker, 1926:195. Type species: *Amnicola lustrica* Pilsbry, 1890:53, by original designation; F. C. Baker, 1926:195.

Fontelicella Gregg and Taylor, 1965:103. Type species: *Fontelicella californiensis* Gregg and Taylor, 1965:109, by original designation; Gregg and Taylor, 1965:104.

Natricola Gregg and Taylor, 1965:108. Type species: *Pomatiopsis robusta* Walker, 1908:97, by original designation; Gregg and Taylor, 1965:109.

Microamnicola Gregg and Taylor, 1965:109. Type species: *Amnicola micrococcus* Pilsbry *in* Stearns, 1893:277, by original designation; Gregg and Taylor, 1965:109.

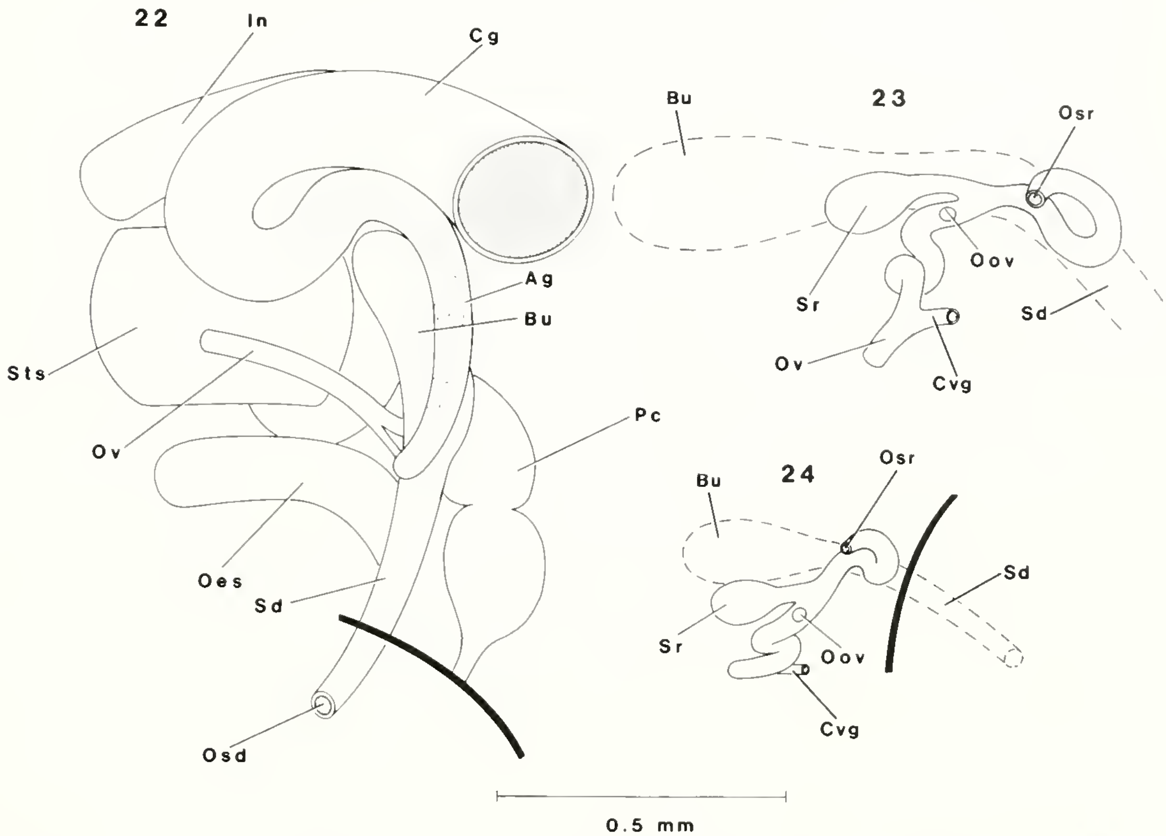

Figure 22. Posterior portion of pallial oviduct and associated organs and structures of *T. clathrata* Stimpson, Moapa Springs, Clark County, NV, USA, USNM 850291, viewed from the right. Note the posterior reflection of the pallial oviduct and small albumen gland (Ag). The thickened curving line indicates the posterior end of the pallial cavity. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, In = intestine, Oes = oesophagus, Osd = opening of the spermathecal duct, Ov = oviduct, Pc = pericardium, Sd = spermathecal duct, Sts = style sac. **Figure 23.** Bursa copulatrix complex of *Tryonia clathrata* (from same lot as above), with the bursa removed (position indicated by dashed lines) in order to reveal the underlying structures. The visceral ganglion connective (Cvg) is tightly pressed against the oviduct. Bu = bursa copulatrix, Cvg = visceral ganglion connective, Oov = opening of oviduct into albumen gland, Ov = oviduct, Osr = opening of seminal receptacle into spermathecal duct, Sd = spermathecal duct, Sr = seminal receptacle. **Figure 24.** Bursa copulatrix complex of *Tryonia acquicostata* (Pilsbry), Alexander Springs, Lake County, FL, USA, UF uncatalogued lot. The thickened curving line indicates the posterior end of the pallial cavity. Bu = bursa copulatrix, Cvg = visceral ganglion connective, Oov = opening of oviduct into albumen gland, Osr = opening of seminal receptacle into spermathecal duct, Sd = spermathecal duct, Sr = seminal receptacle.

Mexistiobia Hershler, 1985:46. Type species: *Mexistiobia manantiali* Hershler, 1985:47, by original designation; Hershler, 1985:46.

Diagnosis: Shell (figures 4–8) globose to elongate-conic, 1.2–8.0 mm in height, with 3.0–6.0 whorls. Aperture simple, sometimes loosened from body whorl. Umbilicus absent to open. Protoconch partly or totally covered with wrinkled pits (Thompson, 1977: fig. 4; Hershler, 1985: fig. 11). Teleoconch smooth or unicarinate on periphery (figure 3), usually with fine growth lines. Radula (figures 25–28) typically taenioglossate, with basal cusps on the central teeth. Mantle and/or penial filament (figures 29, 30, 32, 33) often with distinctive pigment markings. Penis (figures 29–33) with small, distal lobe and narrow, elongate filament. Penial surface with one to fifteen glandular ridges, sometimes on stalked crests. Females oviparous; capsule gland with two tissue sections and a near-terminal opening (figures 34, 35; Thompson, 1977: figs. 5, 7, 10, 11, 18; Hershler, 1985: fig. 14). Oviduct with a single anterior coil on the left side of the albumen gland into which opens the seminal receptacle. Bursa copulatrix typically enlarged and partly posterior to albumen gland; bursa duct and oviduct jointly open into anterior portion of albumen gland.

Species included: *Marstonia agarhecta* Thompson, 1969:243; *Pyrgulopsis archimedis* S. S. Berry, 1947:76; *Fonteliccella californiensis*; *Marstonia castor* Thompson, 1977:130; *Amnicola deserta* Pilsbry, 1916:111; *Marstonia halcyon* Thompson, 1977:128; *Amnicola hendersoni* Pilsbry, 1933:10; *Amnicola idahoensis* Pilsbry, 1933:11; *Pomatiopsis intermedia* Tryon, 1865:220; *Amnicola letsoni* Walker, 1901:113; *Amnicola longinqua* Gould, 1855:130; *Amnicola lustrica*; *Mexistiobia manantiali*; *Amnicola micrococcus*; *Amnicola neomex-

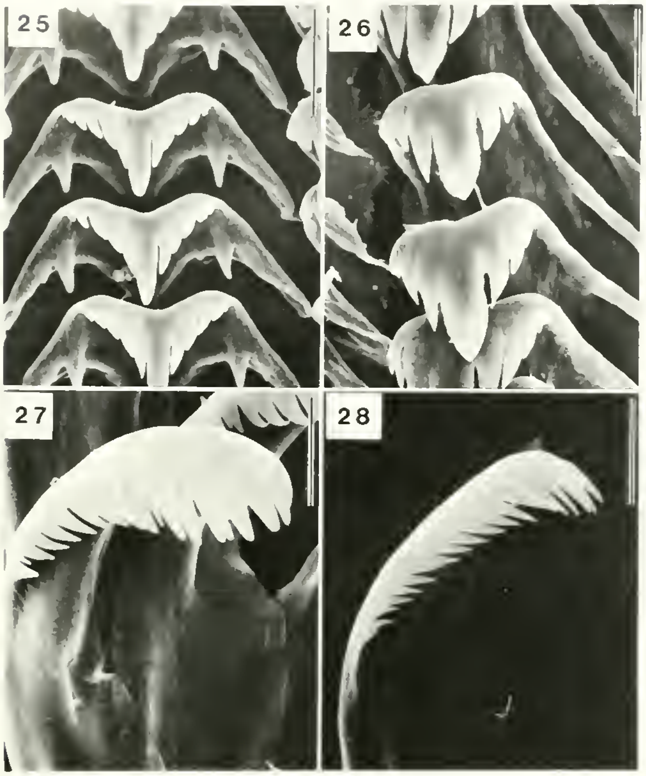

Figure 25. Photograph (SEM) of central radular teeth of *Pyrgulopsis nevadensis* (Stearns), Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot. Scale bar equals 12.0 μm. **Figure 26.** Photograph of lateral teeth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 12.0 μm. **Figure 27.** Photograph of inner marginal tooth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 8.6 μm. **Figure 28.** Photograph of outer marginal tooth of *Pyrgulopsis nevadensis* (Stearns). Scale bar equals 7.5 μm.

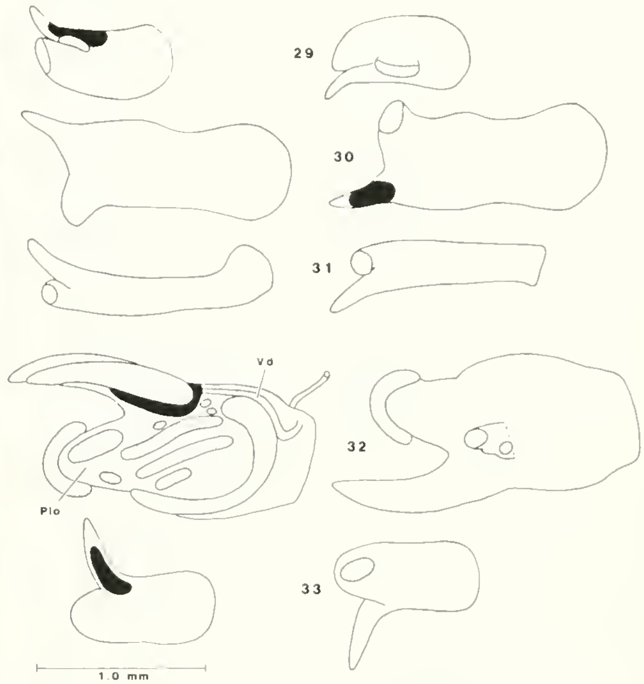

Figure 29. Penis of *Pyrgulopsis nevadensis* (Stearns), south end of Pyramid Lake, Washoe County, NV, USA, UF uncatalogued lot. The dorsal aspect is shown to the left and ventral aspect is on the right. The screened areas indicate glandular ridges whereas the darkened areas are pigmented. **Figure 30.** Penis of *Pyrgulopsis letsoni* (Walker), creek W of Crenshaw Lake, Oakland County, MI, USA, UF 91726. **Figure 31.** Penis of *Pyrgulopsis scalariformis* (Wolf), Meramec River, 12.0 km SE of Leesburg, Crawford County, MO, USA, UF 91727. **Figure 32.** Penis of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292. Plo = penial lobe, Vd = vas deferens. **Figure 33.** Penis of *Pyrgulopsis micrococcus* (Pilsbry), Springdale Springs, Nye County, NV, USA, USNM 850297.

icana Pilsbry, 1916:111; *Marstonia ogmorphaphe* Thompson, 1977:120; *Amnicola olivacea* Pilsbry, 1895: 115; *Pyrgulopsis ozarkensis* Hinkley, 1915:588; *Marstonia pachyta* Thompson, 1977:121; *Amnicola pilsbryi* Baily and Baily, 1952:50; *Pomatiopsis robusta* Walker, 1908:97; *Pyrgula scalariformis* Wolf, 1869:198; *Paludestrina stearnsiana* Pilsbry, 1899:124; *Pyrgulopsis wabashensis* Hinkley, 1908:117.

Fossil species assigned to *Marstonia* and *Fontelicella* by Taylor (1960) and Gregg and Taylor (1965) are not included.

Distribution: *Pyrgulopsis* occurs in much of eastern North America as well as throughout western North America and parts of northern Mexico.

Remarks: Only a limited anatomical study could be made of *Pyrgulopsis nevadensis*, the type species of *Pyrgulopsis*, as only dried bodies were available. We were able to describe its radula (figures 25–28) and penis (figure 29). The species has long been considered endangered (Taylor, 1970) and may now be extinct in the sole locality from which living material was ever found, Pyramid Lake. A recent limnological survey of this locality yielded no live individuals (Galat *et al.*, 1981) of this species, nor were they found during a recent trip to the lake by one of us (F.G.T.).

It is clear from our study that the sole character distinguishing species assigned to *Pyrgulopsis* and other taxa that we consider congeneric is the presence of a peripheral carina on the shell. *Pyrgulopsis* is noteworthy for its diversity in shell and penial morphology. Even within small regions in the Southwest, groups of species show gradations from globose to elongate-conic shells, or gradations from a simple penis with few ridges to a more complex penis with accessory crests and numerous ridges. The eastern species previously assigned to *Marstonia* and *Pyrgulopsis*, united by possession of a penis having few glandular ridges and a broad penial lobe (Berry, 1943: fig. 6; Thompson, 1977: figs. 5, 7, 11, 13, 19, 22, 24), clearly intergrade with western species assigned to *Pyrgulopsis*, *Fontelicella sensu stricto* and *Microamnicola*. We have no doubt that *Pomatiopsis robusta*, the type species of *Natricola*, is also a *Pyrgulopsis*, based on anatomical data given by Gregg and Taylor

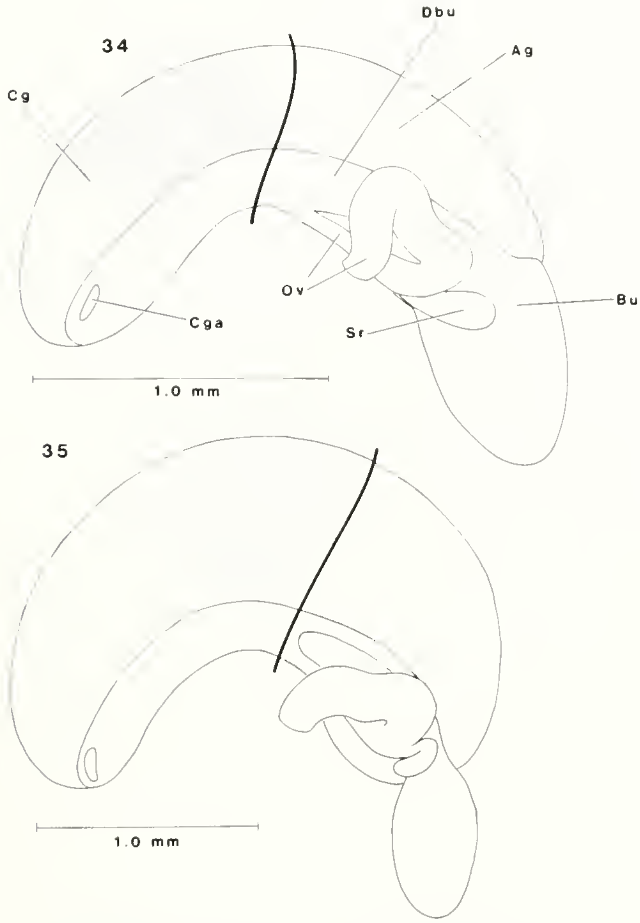

Figure 34. Left lateral aspect of the pallial oviduct and bursa copulatrix complex of *Pyrgulopsis californiensis* (Gregg and Taylor), Campo Creek, San Diego County, CA, USA, USNM 850292. The two tissue sections of the capsule gland (Cg) are indicated by the stippled areas. The thickened curving line indicates the posterior end of the pallial cavity. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cga = capsule gland opening, Dbu = duct of the bursa copulatrix, Sr = seminal receptacle. **Figure 35.** Left aspect of the pallial oviduct and bursa copulatrix complex of *Pyrgulopsis archimedis* S. S. Berry, Upper Klamath Lake, Klamath County, OR, USA, ANSP A602B.

(1965:108). The unique, stunted appearance of the bursa copulatrix complex of *P. manantiali* (Hershler, 1985: fig. 14) is probably a result of the extremely minute size of the snail. In other features such as shell form and penial morphology the species clearly conforms to the *Pyrgulopsis* groundplan.

Among nymphophilines that have received anatomical study, *Pyrgulopsis* is most similar to *Cincinnatia* Pilsbry, 1891, which has a somewhat larger and broader shell as well as a more complex penis having a very small filament, a large number of glandular ridges, and numerous accessory crests (Thompson, 1968: figs. 43–47; Davis & Mazurkiewicz, 1985: figs. 11–15).

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LITERATURE CITED

Ancey, C. F. 1888. Etude monographique sur le genre *Pyrgulopsis*. Bulletins de la Societe Malacologique de France 5:185–202

Arnold, R. 1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Memoirs of the California Academy of Sciences 3:1–420.

Baily, J. L. and R. I. Baily. 1951–52. Further observations on the Mollusca of the relict lakes in the Great Basin. The Nautilus 65:46–53, 85–93.

Baker, F. C. 1926. Nomenclatural notes on American fresh water mollusks. Transactions of the Wisconsin Academy of Science, Arts, and Letters 22:193–205.

Berry, E. G. 1943. The Amnicolidae of Michigan: distribution, ecology, and taxonomy. Miscellaneous Publications of the Museum of Zoology, University of Michigan 57:1–68.

Berry, S. S. 1947. A new *Pyrgulopsis* from Oregon. The Nautilus 60:76–78.

Burch, J. B. 1982. Freshwater snails (Mollusca: Gastropoda) of North America. U.S. Environmental Protection Agency, Contract No. 68-03-1280, EPA-600/3-82-026, 294 p.

Call, R. E. and H. A. Pilsbry. 1886. On *Pyrgulopsis*, a new genus of rissoid mollusk, with descriptions of two new forms. Proceedings of the Davenport Academy of Natural Sciences 5:9–14.

Davis, G. M. and M. Mazurkiewicz. 1985. Systematics of *Cincinnatia winkleyi* (Gastropoda: Hydrobiidae). Proceedings of the Academy of Natural Sciences of Philadelphia 137:28–47.

Davis, G. M., M. Mazurkiewicz, and M. Mandracchia. 1982. *Spurwinkia*: morphology, systematics, and ecology of a new genus of North American marshland Hydrobiidae (Mollusca: Gastropoda). Proceedings of the Academy of Natural Sciences of Philadelphia 134:143–177.

Galat, D. L., E. L. Lider, S. Vigg, and S. R. Robertson. 1981. Limnology of a large, deep North American terminal lake, Pyramid Lake, Nevada, U.S. Hydrobiologia 82:281–317.

Gould, A. A. 1855. New species of land and freshwater shells from western (N.) America. Proceedings of the Boston Society of Natural History 5:127–130.

Gregg, W. V. and D. W. Taylor. 1965. *Fontelicella* (Prosobranchia: Hydrobiidae), a new genus of West American freshwater snails. Malacologia 3:103–110.

Hershler, R. 1985. Systematic revision of the Hydrobiidae (Gastropoda: Rissoacea) of the Cuatro Cienegas Basin, Coahuila, Mexico. Malacologia 26:31–123.

Hinkley, A. A. 1908. A new species of *Pyrgulopsis*. The Nautilus 21:117–118.

Hinkley, A. A. 1915. New fresh-water shells from the Ozark Mountains. Proceedings of the United States National Museum 49:587–589.

Leonard, A. B. and T.-Y. Ho. 1960a. New *Calipyrgula* from

Pleistocene of Texas and notes on *Cochliopa riograndensis*. The Nautilus 73:125–129.

Leonard, A. B. and T.-Y. Ho. 1960b. A new species of *Calipyrgula* (Hydrobiidae) from the Pleistocene of Texas. The Nautilus 73:110–113

Morrison, J. P. E. 1945. *Durangonella*, a new hydrobiine genus from Mexico, with three new species. The Nautilus 59:18–23.

Pilsbry, H. A. 1889. New and little known American mollusks. No. 1. Proceedings of the Academy of Natural Sciences of Philadelphia 41:81–89.

Pilsbry, H. A. 1890. Notices of new Amnicolidae. The Nautilus 4:63–64.

Pilsbry, H. A. 1895. New American freshwater mollusks. The Nautilus 8:114–116.

Pilsbry, H. A. 1899. Catalogue of the Amnicolidae of the western United States. The Nautilus 12:121–127.

Pilsbry, H. A. 1916. New species of *Amnicola* from New Mexico and Utah. The Nautilus 29:111–112.

Pilsbry, H. A. 1933. Amnicolidae from Wyoming and Oregon. The Nautilus 47:9–12.

Pilsbry, H. A. 1935. Western and southwestern Amnicolidae and a new *Humboldtiana*. The Nautilus 48:91–94.

Pilsbry, H. A. 1952. *Littoridina tenuipes* (Couper). The Nautilus 66:50–54.

Pilsbry, H. A. and J. H. Ferriss. 1906. Mollusca of the southwestern states. II. Proceedings of the Academy of Natural Sciences of Philadelphia 58:123–175.

Russell, R. H. 1971. Mollusca of Fish Springs, Juab County, Utah: rediscovery of *Stagnicola pilsbryi* (Hemphill, 1890). Great Basin Naturalist 31:223–236.

Stearns, R. E. C. 1883. Description of a new hydrobiinoid gasteropod from the mountain lakes of the Sierra Nevada, with remarks on allied species and the physiographic features of said region. Proceedings of the Academy of Natural Sciences of Philadelphia 35:171–176.

Stearns, R. E. C. 1893. Report on the land and fresh-water shells collected in California and Nevada by the Death Valley Expedition, including a few additional species obtained by Dr. C. Hart Merriam and assistants in parts of the southwestern United States. North American Fauna 7:269–283.

Stimpson, W. 1865. Researches upon the Hydrobiinae and allied forms. Smithsonian Miscellaneous Collections 201: 1–59.

Taylor, D. W. 1960. Late Cenozoic molluscan faunas from the High Plains. U.S. Geological Survey Professional Papers 337:1–94.

Taylor, D. W. 1966. A remarkable snail fauna from Coahuila, Mexico. The Veliger 9:152–228.

Taylor, D. W. 1970. 4. Western freshwater mollusks. *In:* Clarke, A. H. (ed.). Proceedings of the American Malacological Union Symposium on Rare and Endangered Mollusks. Malacologia 10:33–34.

Taylor, D. W. 1983. Status investigation of mollusks. Report to the New Mexico Department of Game and Fish, Contract Nos. 519-69-01, 519-69-01A, 81 p.

Thompson, F. G. 1968. The aquatic snails of the family Hydrobiidae of peninsular Florida. University of Florida Press, Gainesville, FL, xv + 268 p.

Thompson, F. G. 1969. Some hydrobiid snails from Georgia and Florida. Quarterly Journal of the Florida Academy of Science 32:242–265.

Thompson, F. G. 1977. The hydrobiid snail genus *Marstonia*. Bulletin of the Florida State Museum, Biological Sciences 21:113–158.

Thompson, F. G. 1979. The systematic relationships of the hydrobiid snail genus *Nymphophilus* Taylor 1966 and the status of the subfamily Nymphophilinae. Malacological Review 12:41–49.

Thompson, F. G. 1984. North American freshwater snail genera of the hydrobiid subfamily Lithoglyphinae. Malacologia 25:109–141.

Thompson, F. G. and J. E. McCaleb. 1978. A new freshwater snail from a spring in eastern Alabama. American Midland Naturalist 100:350–358.

Tryon, G. W. 1865. Descriptions of new species of *Amnicola*, *Pomatiopsis*, *Somatogyrus*, *Gabbia*, *Hydrobia*, and *Rissoa*. Journal of Conchology 1:219–222.

Walker, B. 1901. A new species of *Amnicola*. The Nautilus 14:113–114

Walker, B. 1908. *Pomatiopsis robusta* n. sp. The Nautilus 21:97.

Wolf, J. 1869. Descriptions of three new species of shells. American Journal of Conchology 5:198.

Ecological Differentiation Within the Genus *Helisoma* (Gastropoda: Planorbidae) in Central Canada

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ABSTRACT

The distributions of *Helisoma anceps*, *H. campanulatum*, *H. corpulentum*, *H. pilsbryi infracarinatum*, and *H. trivolvis* were examined in relation to water body and substrate type, eight water chemistry parameters, *Helisoma* species diversity (HSD), total gastropod diversity (TGD), and macrophyte diversity (MD). A total of 310 of the 437 sites studied contained *Helisoma*. Significant interspecific differences existed with respect to the most frequented types of water bodies and substrates, as well as with respect to ecological tolerance ranges for total dissolved solids, total alkalinity, phosphorus, nitrate, sulphate, dissolved organic matter, and chloride. These differences were reflected in the geographical distributions of the species. *Helisoma trivolvis* was the most widespread species within the study area, and showed the broadest ecological tolerance ranges for the parameters examined, while *H. campanulatum* was the most restricted in terms of habitat parameters, and was found primarily on the Precambrian Shield. *Helisoma anceps* occupied an intermediate position between these two species. *Helisoma corpulentum* and *H. p. infracarinatum* were rare in the study area. Geographical range extensions are presented for *H. a. royalense*, *H. corpulentum*, and *H. campanulatum*.

Multiple regression analysis showed that sulphate, dissolved organic matter, and chloride together accounted for *ca.* 10% of the variability in HSD. HSD was positively correlated with TGD and MD. Significant interspecific differences existed with respect to HSD and MD, but not TGD. Ecological differences between species of the same genus may reduce competition where geographical ranges overlap and may be an important factor in divergent evolution.

INTRODUCTION

The geographical boundaries of the distributions of several planorbid species are located in central Canada, an area which also contains a number of important geologic interfaces. The genus *Helisoma* is of particular interest, since in this region it is represented by all five species [as currently understood (*e.g.*, Clarke, 1981)] native to Canada: *H. anceps* Menke, 1830, *H. campanulatum* Say, 1821, *H. corpulentum* Say, 1824, *H. pilsbryi* Baker, 1926, and *H. trivolvis* Say, 1816.

Although the ranges of these species overlap in central Canada, preliminary observations have suggested that often only one or two species of this genus may be present in any given habitat. It was therefore the objective of the present study to determine whether the latter suspicion was indeed true, and if so, whether the distributions of individual species could be differentiated with respect to common habitat descriptors such as water body type, bottom substrate, and water chemistry. The ecology of *Helisoma* species is thus far known primarily in qualitative terms (*e.g.*, Baker, 1932, 1936, 1945; Clarke, 1973, 1981); some quantitative data have been reported for the study area by Pip (1978, 1985, 1986).

THE STUDY AREA

The present study was carried out within the area bounded by 47° and 54°N, and 94° and 106°W. This region is geologically diverse. The Precambrian Shield, which consists largely of granitic and gneissic volcanic rock, dominates the eastern portion of the study area east of Lake Winnipeg. The area west of Lake Winnipeg and including much of Lakes Winnipegosis and Manitoba is underlain mainly by Ordovician, Silurian, and Devonian sedimentary rocks, particularly limestone and dolomite. West of the latter two lakes these sedimentary rocks are of more recent Triassic and Cretaceous origin. Irregular deposits of Cenozoic shales occur in the southwestern portion of the study area. The waters of the Precambrian Shield are typically low in dissolved inorganic materials (Pip, 1985), but west of the Shield boundary, total alkalinity and dissolved solids tend to show higher values.

MATERIALS AND METHODS

A total of 437 sites was examined within the study area during the May–September seasons of 1972–85. Of these, 41% were lakes (> 10 ha), 42% ponds (< 10 ha), 9% rivers (> 2 m deep), and 8% creeks (< 2 m deep). Because of environmental heterogeneity, large lakes were sampled at a number of different stations, which were each treated as separate sites. All sites contained water year-round.

While heterogeneous substrate types were present at

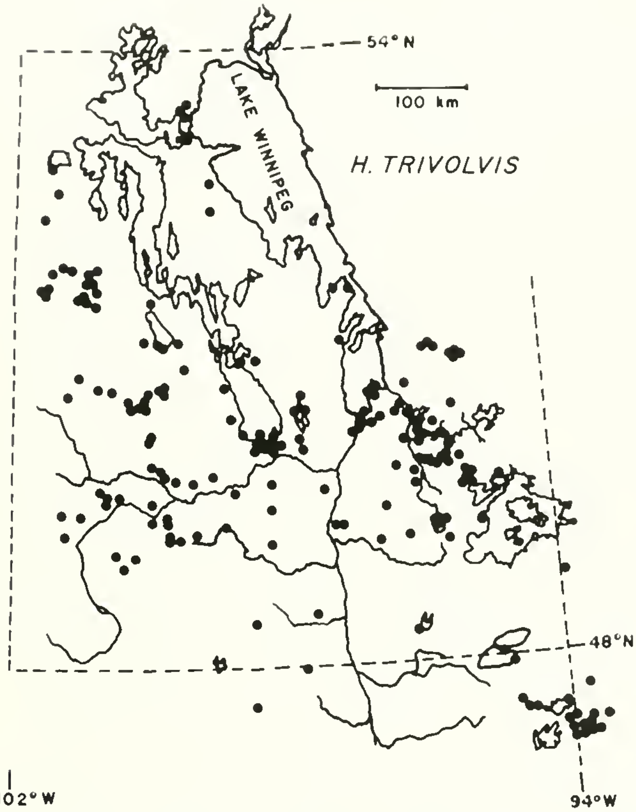

Figure 1. Distribution of sites where *H. trivolvis* was recorded.

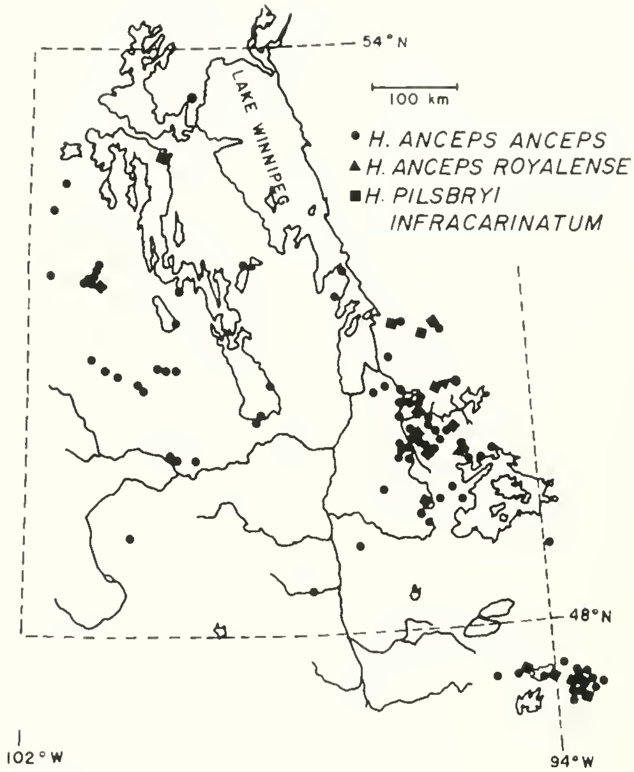

Figure 2. Distribution of sites where *H. anceps* and *H. pilsbryi infracarinatum* were recorded.

many sites, habitats were classified according to the predominant substrates present where the snails were found. Approximately 11% of the water bodies sampled had primarily granitic bedrock bottom, 2% limestone bedrock, 1% shale, 16% a mixture of gravel and coarse sand, 27% sand, 6% silt, 19% clay, and 18% mainly organic substrates such as peat.

Shallow sites were examined for the presence of molluscs and aquatic macrophytes by wading, while deeper waters were sampled by dredging with a rake from a small boat, or, at depths of > 3 m, by using SCUBA. Search time at each site was limited to 1 hr. Plant material was taken to the laboratory, washed, and examined for additional snails. Only macrophytes that were at least partially submerged were scored. Diversity was defined as the number of species present.

Surface water samples were collected for most sites, although at depths of > 3 m a van Dorn sampler was used. The samples were placed on ice in darkness and frozen within a maximum of 48 hr. Samples were analyzed using methods recommended by the American Public Health Association (1971). The pH was measured *in situ* with a portable pH meter.

While most sites were visited only once, approximately 50 locations were resampled at different times of the season and in different years. For these sites, extreme low and high water chemistry parameter values were used for statistical analysis. The critical significance level for all statistical procedures in the present study was $p = 0.05$.

RESULTS

Distribution

Of the 437 cases examined, 310 contained a record of one or more *Helisoma* species. *Helisoma trivolvis* was the most frequently observed member of this genus and was widely distributed throughout the study region (figure 1), occurring at approximately 44% of the sites visited. Clarke (1981) recognized two subspecies of *H. trivolvis* in the area under consideration: *H. t. trivolvis* east of Manitoba (except for a small region in central Saskatchewan) and *H. t. subcrenatum* Carpenter, 1856 in Manitoba and to the west. In the present study this zoogeographical separation was not found to be quite as distinct; both forms occurred in southern Manitoba, although *H. t. subcrenatum* was much more common. These two forms are usually distinguished by differences in axial height (Clarke, 1981), but large series examined at certain sites (*e.g.*, Jackson Lake, near Sidney in southwestern Manitoba) showed a wide range of this character, suggesting that further study is needed regarding the status of these two forms.

Helisoma anceps was also widely distributed in the study area, although it was less common in the southwestern portion (figure 2). It was found at 24% of the sites sampled. While *H. a. anceps* formed the majority

of the occurrences of this species, two populations of *H. a. royalense* Walker, 1909 were found in eastern Manitoba (West Hawk Lake in Whiteshell Provincial Park and Bird Lake in Nopiming Provincial Park), representing a westward range extension for this taxon from its previously known boundary in northwestern Ontario.

Helisoma campanulatum (figure 3) was distributed primarily on the Precambrian Shield. Occurrences west of the Shield were sporadic, but these constituted southwestward extensions of the range reported by Clarke (1981). The bulk of the populations encountered consisted of *H. c. campanulatum,* although a few occurrences of *H. c. collinsi* Baker, 1939 were noted in the southeastern portion of the study area. This species showed a wide range of morphology and size at different sites.

Helisoma pilsbryi infracarinatum Baker, 1932 was infrequently found in the present study (4% of sites sampled). It was not seen in the southwestern portion of the study area (figure 2).

Helisoma corpulentum was very rare in the study area and was found at only 1% of the sites visited. It was found at a few stations on the Winnipeg River in southeastern Manitoba, and in Whitefish Lake, located on the Manitoba-Saskatchewan border in the Porcupine Provincial Forest, approximately 400 km west of its nearest Winnipeg River occurrence, thus constituting a range extension (figure 3). The Whitefish Lake locus, so far as is known, was not linked by intervening occurrences to the Winnipeg River populations and may possibly have been the result of accidental transport by human agency, since this lake is frequented by tourist sport fishermen. However, *H. corpulentum* was common in the lake and therefore must have existed there for some time.

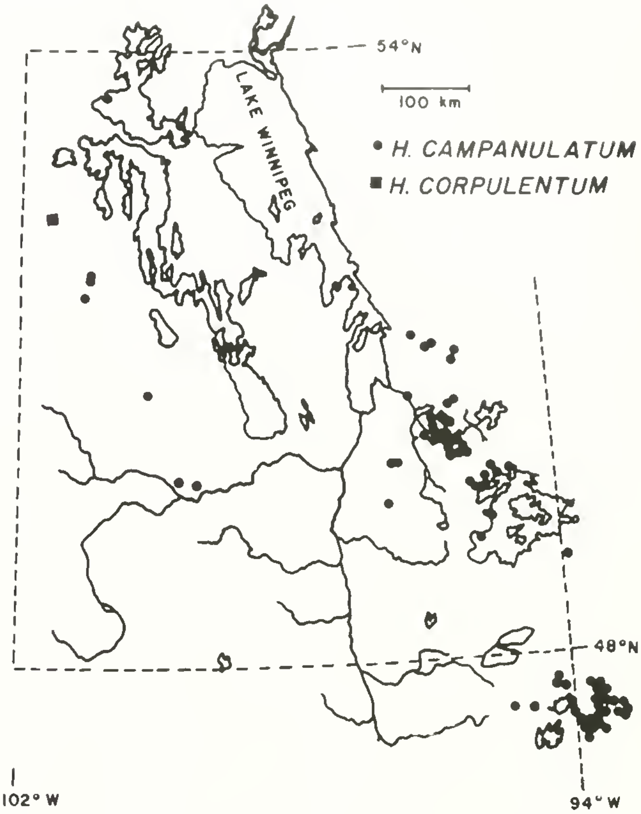

Figure 3. Distribution of sites where *H. campanulatum* and *H. corpulentum* were recorded.

Community Diversity

The mean number of *Helisoma* species (HSD) found at the same site was lowest for sites containing *H. trivolvis* and highest for sites where *H. pilsbryi infracarinatum* was observed (table 1). HSD was compared for the four most frequent species; one-way analysis of variance was used, since Cochran's C and Bartlett-Box F tests indicated that the homogeneity of variance assumption required for this test was valid. The F ratio between the species was highly significant (table 2), suggesting that the respective species differed in their tendency to occur in communities where other members of the genus were present. Different species pairs were further examined using Duncan's, Student-Newman-Keuls, Tukey's "honestly significant difference," and Scheffé's multiple comparison procedures (Winer, 1971). The results (table 2) showed that *H. trivolvis* and *H. p. infracarinatum* each differed from the other three species with respect to HSD.

When the four species were compared with respect to the total numbers of gastropod species recorded at each site (TGD), there were no significant differences between them (table 2). However, comparisons of aquatic

Table 1. Mean HSD, TGD, and MD values for sites where each *Helisoma* species occurred. Values in parentheses are standard errors

Species	HSD	TGD	MD	N
H. trivolvis	1.53 (0.05)	5.80 (0.20)	7.39 (0.35)	200
H. anceps	1.73 (0.08)	5.61 (0.28)	7.33 (0.45)	113
H. campanulatum	1.83 (0.09)	6.36 (0.35)	11.95 (0.52)	92
H. pilsbryi infracarinatum	2.52 (0.20)	6.95 (0.76)	9.10 (1.29)	21
H. corpulentum	2.0	5.0	9.5	4
Total sites	0.95 (0.05)	4.58 (0.14)	6.96 (0.22)	430

Table 2. Results of one-way analysis of variance and species-pair comparisons with respect to community diversity for the four most frequent species.

Diversity parameter	Significance of F ratio among four species	Species pairs significantly ($p < 0.05$) different
No. of *Helisoma* spp. at same site (HSD)	$F = 11.6$ $p < 0.001$*	*H. trivolvis vs. H. campanulatum*[1,2,3,4] *H. trivolvis vs. H. anceps*[1,2] *H. trivolvis vs. H. p. infracarinatum*[1,2,3,4] *H. p. infracarinatum vs. H. anceps*[1,2,3,4] *H. p. infracarinatum vs. H. campanulatum*[1,2,3,4]
Total gastropod diversity at same site (TGD)	$F = 2.03$ $p = 0.11$	None
Macrophyte diversity at same site (MD)	$F = 20.1$ $p < 0.001$*	*H. campanulatum vs. H. anceps*[1,2,3,4] *H. campanulatum vs. H. trivolvis*[1,2,3,4] *H. campanulatum vs. H. p. infracarinatum*[1,2]

[1] Duncan.
[2] Student-Newman-Keuls.
[3] Tukey "honestly significant difference".
[4] Scheffé.
* Significant difference.

macrophyte species richness (MD) yielded a highly significant F ratio that was largely attributed to differences between *H. campanulatum* and the other three species (table 2).

HSD was highly significantly correlated with TGD ($r = 0.56$, $p < 0.001$, $N = 430$) and with MD ($r = 0.32$, $p < 0.001$, $N = 430$) recorded at the same sites. TGD and MD were also correlated with each other ($r = 0.26$, $p < 0.001$, $N = 430$).

Chi-square tests were applied to determine whether any of the species appeared to be associated with others. The results (table 3) showed that most species pairs were not significantly associated. Only two significant positive associations were found: *H. trivolvis* with *H. pilsbryi infracarinatum*, and *H. campanulatum* with *H. corpulentum*. In both cases the second species was rare. Thus the three most common species did not tend to occur with each other at the same site, suggesting that they frequented different habitats within the study area. Because of the low frequencies of *H. p. infracarinatum* and *H. corpulentum*, these taxa were excluded from further analysis; what is known of their habitat characteristics within the study area has been summarized by Pip (1986).

Water Body and Substrate Type

The distributions of the three common species were examined with respect to water body type by using 2 × 4 chi-square tests to compare the number of occurrences in each of the four cells for sites where each species was present and those where it appeared to be absent. These groups are henceforth designated as "found" sites and "remaining" sites, respectively. "Remaining" sites were used for comparison rather than the overall site sampling distribution because the more frequently a species occurs, the more its distribution pattern approaches that of the overall sampling distribution. In the study area both *H. anceps* and *H. campanulatum* showed significantly different distributions at found sites compared to the remaining sites (figure 4). *Helisoma anceps* was moderately and *H. campanulatum* strongly more frequent in lakes than would be expected from the sampling distribution. *Helisoma campanulatum* also occurred the most frequently of the three species in rivers, but was not found in creeks. *Helisoma anceps* occurred less frequently in lotic waters. *Helisoma trivolvis* did not appear to show any distinct preference with respect to water body type.

Table 3. Results of chi-square tests for interspecific association. Upper diagonal = chi-square, lower diagonal = p. N = 437.

	H. trivolvis	*H. anceps*	*H. campanulatum*	*H. p. infracarinatum*	*H. corpulentum*
H. trivolvis	x	0.04	0.49	12.76	0.62
H. anceps	0.83	x	1.92	1.71	< 0.01
H. campanulatum	0.48	0.17	x	2.05	8.23
H. p. infracarinatum	< 0.001*	0.19	0.15	x	0.18
H. corpulentum	0.43	0.97	< 0.01*	0.67	x

* Significant positive correlation

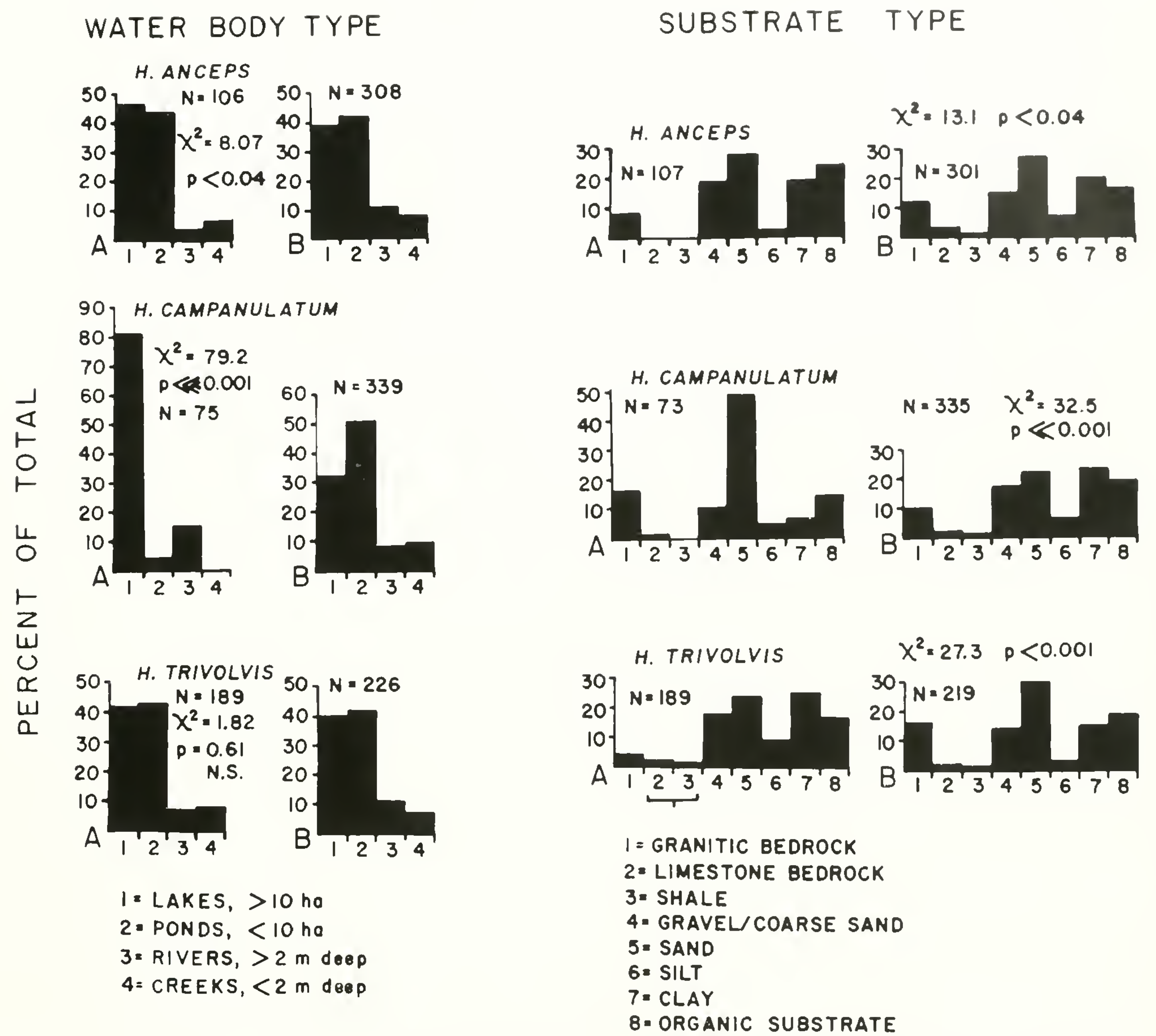

Figure 4. Comparisons of sampling distributions for water body type and bottom substrate type of found (A) and remaining (B) sites for the three most frequent species. Horizontal brackets indicate the cells that were combined for chi-square analysis for all species. N.S. = no significant difference.

Further comparisons were made among species by using chi-square tests for each possible species pair (table 4). *Helisoma campanulatum* differed highly significantly in distribution from both *H. anceps* and *H. trivolvis*; it was primarily a lacustrine species and seldom occurred in ponds. The latter two species each occurred with approximately equal frequencies in lakes and ponds. *Helisoma anceps* and *H. trivolvis* did not differ significantly from each other.

Distribution with respect to predominant substrate type was compared at found *vs.* remaining sites using 2 × 6 chi-square tests (figure 4). Substrate type was divided into six cells; limestone and shale categories were combined in order to raise the theoretical frequencies and to avoid zero column sums in the contingency tables. All three species showed significantly different distributions at found sites compared to remaining sites, and also when compared to each other (table 4). *Helisoma campanulatum* showed a strong preference for sand. *Helisoma trivolvis* tended to be more frequent on clay, and *H. anceps* on highly organic substrates compared to remaining site frequencies.

Water Chemistry

Distributions of water chemistry parameters were first examined using preliminary chi-square tests. Extreme low and high parameter values were included for sites

Table 4. Results of species-pair chi-square comparisons with respect to water body and bottom substrate type for the three most frequent species. Upper diagonal = chi-square, lower diagonal = p

	H. trivolvis	*H. anceps*	*H. campanulatum*
A. Water body type			
H. trivolvis	x	3.02	50.7
H. anceps	0.61	x	46.4
H. campanulatum	< 0.001*	< 0.001*	x
Overall chi-square = 57.5, p < 0.001*			
B. Bottom substrate type			
H. trivolvis	x	14.4	36.5
H. anceps	0.03*	x	20.5
H. campanulatum	< 0.001*	< 0.001*	x
Overall chi-square = 47.9, p < 0.001*			

* Significant difference.

that were sampled a number of times. The distributions were divided into six cells for all factors except chloride and sulphate, which were assigned three and four cells, respectively.

All three species showed significantly different distributions for total dissolved solids at found sites compared to remaining sites (figure 5). *Helisoma campanulatum* showed the greatest affinity for low values, while *H. trivolvis* appeared to tolerate the highest concentrations. The differences between these two species can be seen in the similarity of the distributions of the found sites for *H. trivolvis* and the remaining sites for *H. campanulatum* in figure 5. Total alkalinity showed trends similar to those seen for total dissolved solids (figure 5).

Molybdenum reactive phosphorus was significantly different at found and at remaining sites for all species (figure 6). The greatest proportion of found sites in the lowest concentration class was seen for *H. anceps*. However, *H. campanulatum* showed the lowest mean value because *H. anceps* could also occur at sites with higher values than the maximum seen for *H. campanulatum*. *Helisoma trivolvis* showed the highest percentage of sites with high values.

Significant differences for combined nitrate and nitrite were observed at found and at remaining sites only for *H. campanulatum* and *H. trivolvis* (figure 6). *Helisoma campanulatum* showed the greatest frequencies at the lower end of the concentration scale, while *H. trivolvis* showed the greatest proportion of higher values.

The pH was significantly different at found and at remaining sites only for *H. campanulatum* (figure 7), which showed the narrowest range of values of the three species. Chloride appeared to be important for *H. campanulatum* (figure 7), which occurred exclusively at sites with low values of this parameter. Chi-square values were very small for the other two species.

Sulphate was a significant parameter for *H. campanulatum* and *H. trivolvis* (figure 8). The former was limited (with one exception) to the lowest concentration cell, while the latter tolerated a broad range of values.

Dissolved organic matter was significant for all species

Table 5. Results of Kruskal-Wallis one-way analysis of variance and species-pair comparisons with respect to water chemistry parameters for the three most frequent species.

Parameter	Chi-square, corrected for ties	Species pairs significantly different (p < 0.05)
pH	0.38, p = 0.83	None
Total dissolved solids	62.1, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2,3,4]
		H. anceps vs. H. campanulatum[1]
Total alkalinity	54.9, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2,3,4]
		H. anceps vs. H. campanulatum[1,2,3,4]
Molybdenum reactive phosphorus	9.16, p = 0.01*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2,3]
Nitrate and nitrite	15.0, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2,3]
Chloride	29.9, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2]
Sulphate	39.1, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2,3,4]
		H. anceps vs. H. campanulatum[1]
Dissolved organic matter	15.0, p < 0.001*	*H. trivolvis vs. H. campanulatum*[1,2,3,4]
		H. trivolvis vs. H. anceps[1,2]

[1] Duncan.
[2] Student-Newman-Keuls.
[3] Tukey "honestly significant difference".
[4] Scheffé.
* Significant difference.

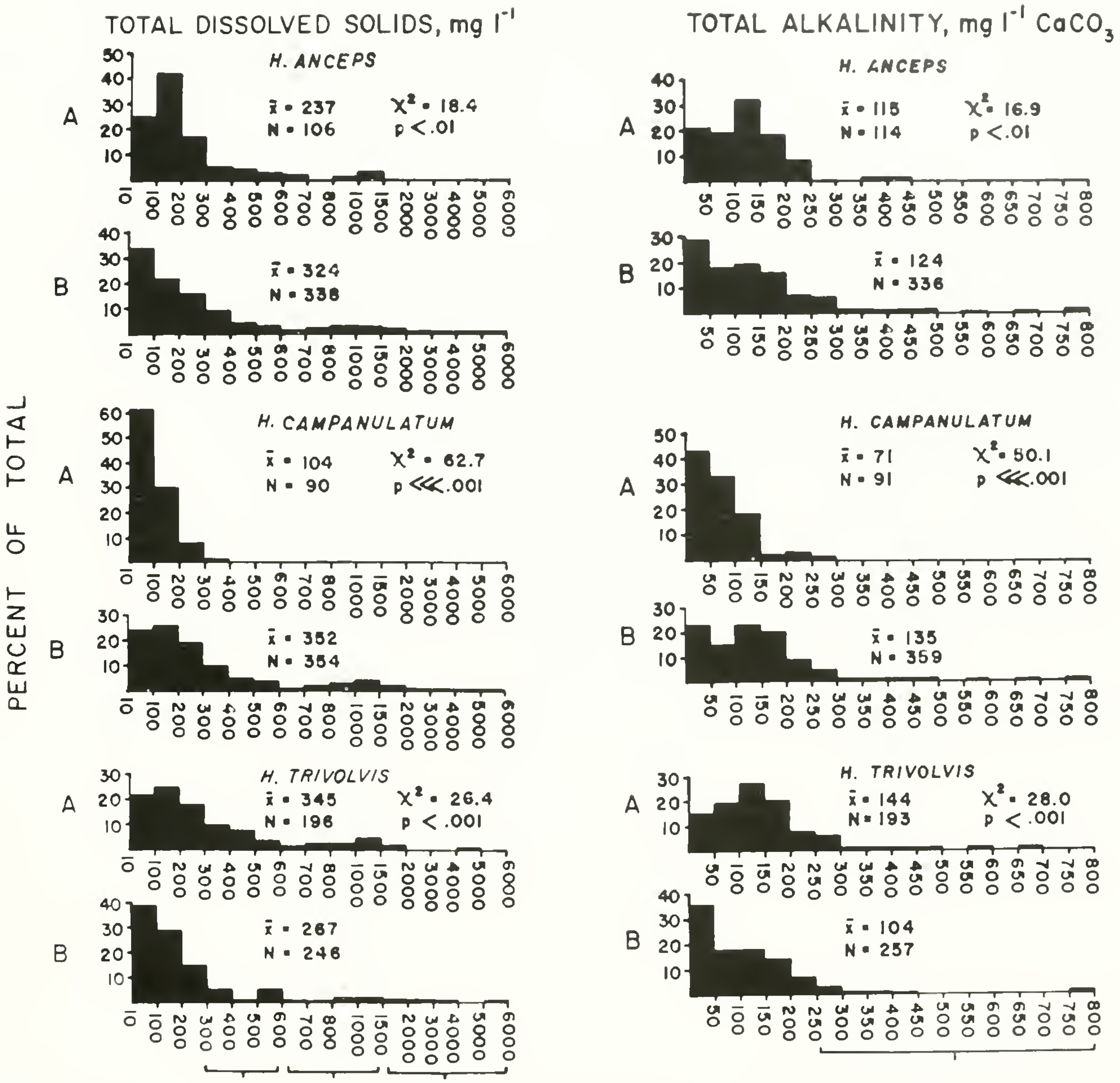

Figure 5. Comparisons of sampling distributions for total dissolved solids and total alkalinity of found (A) and remaining (B) sites for the three most frequent species. Horizontal brackets indicate the cells that were combined for chi-square analysis for all species.

at found *vs.* remaining sites (figure 8). As had been seen for total dissolved solids, again the distribution of remaining sites for *H. campanulatum* resembled the distribution of found sites for *H. trivolvis*.

The water chemistry parameters were examined further for interspecific differences among the three most frequent species. Since several water chemistry parameters did not show normal sampling distributions, non-parametric multiple comparisons were made for all parameters using Kruskal-Wallis one-way analysis of variance. The results indicated that all parameters except pH showed significant interspecific differences (table 5). Each species pair was then compared using Duncan's, Student-Newman-Keuls, Tukey's "honestly significant difference," and Scheffé's multiple comparison tests. The results showed significant pair differences for all variables except pH (table 5). *Helisoma trivolvis* differed significantly from *H. campanulatum* and from *H. anceps* with respect to total dissolved solids, total alkalinity, phosphorus, combined nitrate and nitrite, sulphate, and dissolved organic matter. *Helisoma trivolvis* also differed from *H. campanulatum* with respect to chloride. *Helisoma anceps* differed from *H. campanulatum* with respect to fewer chemical parameters; these were: total alkalinity (most significant) and, at reduced levels of significance, total dissolved solids and sulphate.

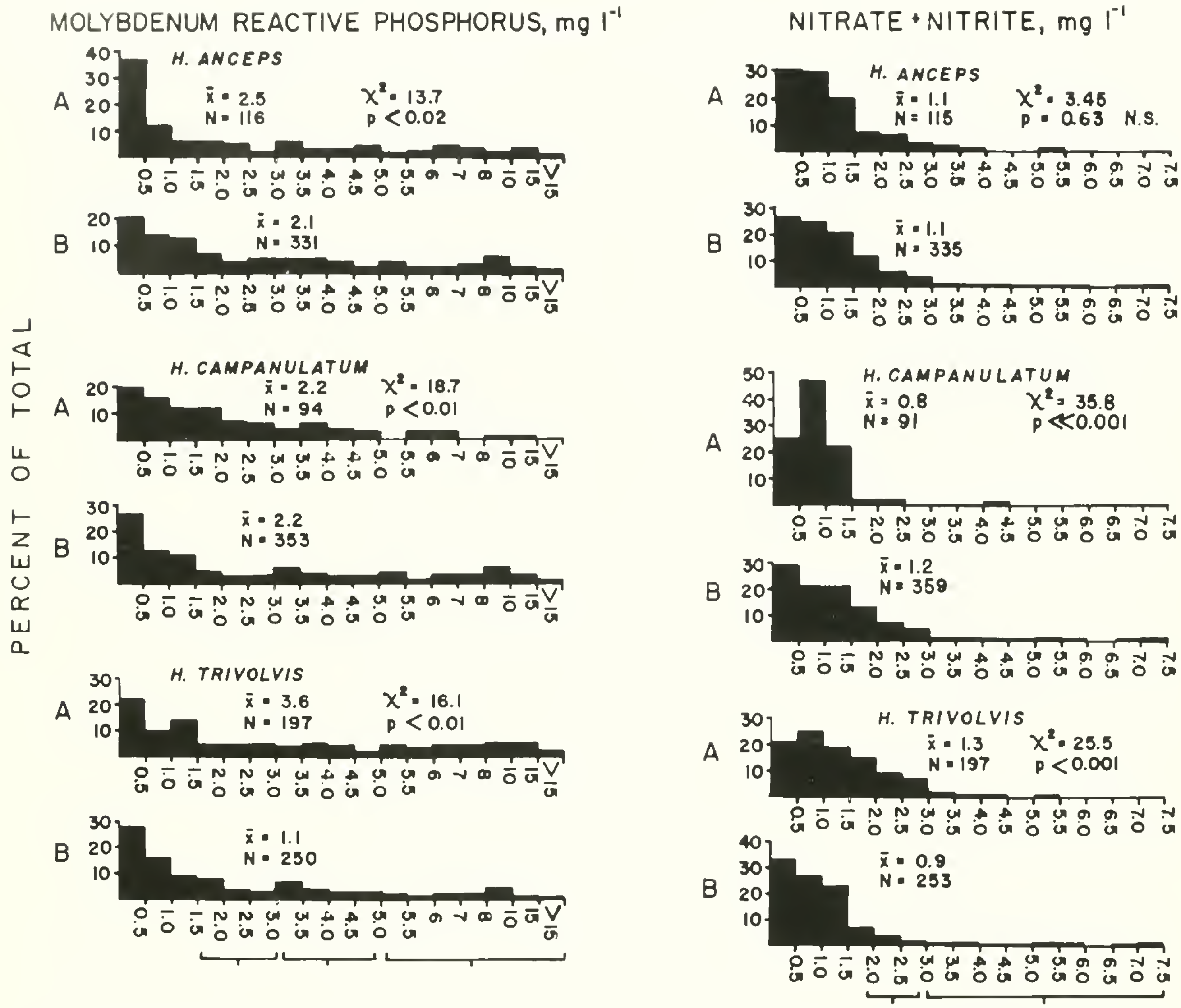

Figure 6. Comparisons of sampling distributions for molybdenum reactive phosphorus and combined nitrate and nitrite of found (A) and remaining (B) sites for the three most frequent species. Horizontal brackets indicate the cells that were combined for chi-square analysis for all species. N.S. = no significant difference.

The relative importance of the different water chemistry parameters could not be defined, since the latter showed a high degree of intercorrelation (table 6). HSD was significantly inversely correlated with dissolved organic matter, total dissolved solids, chloride, and total alkalinity (table 6). Stepwise multiple regression of untransformed water chemistry parameters on HSD as the dependent variable admitted two parameters into the regression equation, which together accounted for only 4% of the observed variability in HSD: dissolved organic matter ($R^2 = 0.03$ after step 1) and chloride ($R^2 = 0.04$ after step 2) ($p = 0.0001$, $N = 479$). Respective beta values were -0.17 and -0.12, indicating that dissolved organic matter was more important.

When HSD and the chemical parameters (except pH) were log transformed, correlation with total dissolved solids improved substantially when compared with the corresponding values for untransformed variables (table 6), and new significant inverse correlations emerged for sulphate and combined nitrate and nitrite. Apparently these relationships were nonlinear. Stepwise multiple regression of untransformed variables (except pH) admitted sulphate alone into the equation ($R^2 = 0.05$, $p = 0.020$, $N = 479$).

DISCUSSION

The results of the present study suggested that the three most common *Helisoma* species coexist within the study area by frequenting habitats with somewhat different physical and chemical characteristics. Within the study area the major factors that differed between *H. trivolvis*

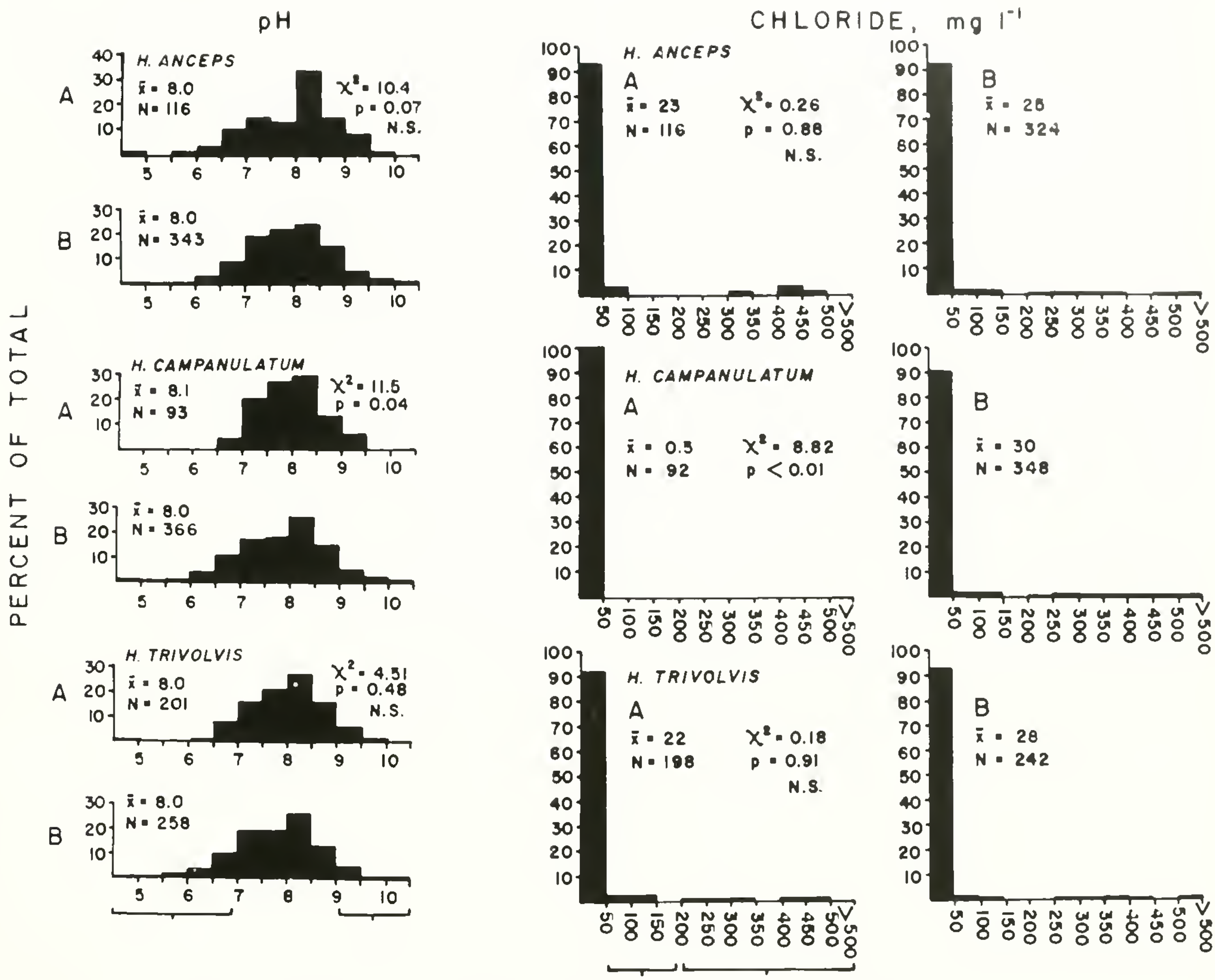

Figure 7. Comparisons of sampling distributions for pH and chloride of found (A) and remaining (B) sites for the three most frequent species. Horizontal brackets indicate the cells that were combined for chi-square analysis for all species. N.S. = no significant difference.

and *H. campanulatum* were: habitat type, substrate type, total dissolved solids, total alkalinity, phosphorus, nitrate/nitrite, sulphate, chloride, and dissolved organic matter. *Helisoma trivolvis* differed from *H. anceps* with respect to fewer factors; these were: substrate type, total dissolved solids, total alkalinity, phosphorus, nitrate/nitrite, and sulphate. *Helisoma campanulatum* and *H. anceps* differed with respect to the fewest factors: habitat type, substrate type, total alkalinity, total dissolved solids, and sulphate. In addition, *H. campanulatum* tended to occupy habitats that had a much higher macrophyte species richness than those frequented by other species. These observations explained to a large extent the geographical distributions of these species. *Helisoma campanulatum*, with its significant preference for lakes and rivers, sand substrates, low water chemistry parameter values, and high macrophyte diversity, was found mainly on the Precambrian Shield, where such habitat characteristics were common. *Helisoma anceps*, with less stringent requirements, occupied a correspondingly broader area. Its significant but reduced preference for lakes (compared to *H. campanulatum*), decreased frequency in lotic waters, and greater tolerance of rather higher water chemistry parameter values was reflected in its greater frequencies in waters west of the Shield, even though it was still much more common in Shield waters, where low parameter values predominated.

Because of the reduced number of low-value water chemistry parameter sites west of the Shield, *H. anceps* and *H. campanulatum* often occurred together at these sites, and therefore appeared to be associated when a subset of data containing a high proportion of non-Shield sites was considered (Pip, 1978). However, such association was not apparent on the Shield (Pip, 1985).

Helisoma trivolvis showed the widest tolerance ranges for water chemistry values and could occupy all water body and bottom substrate types. The broader variety

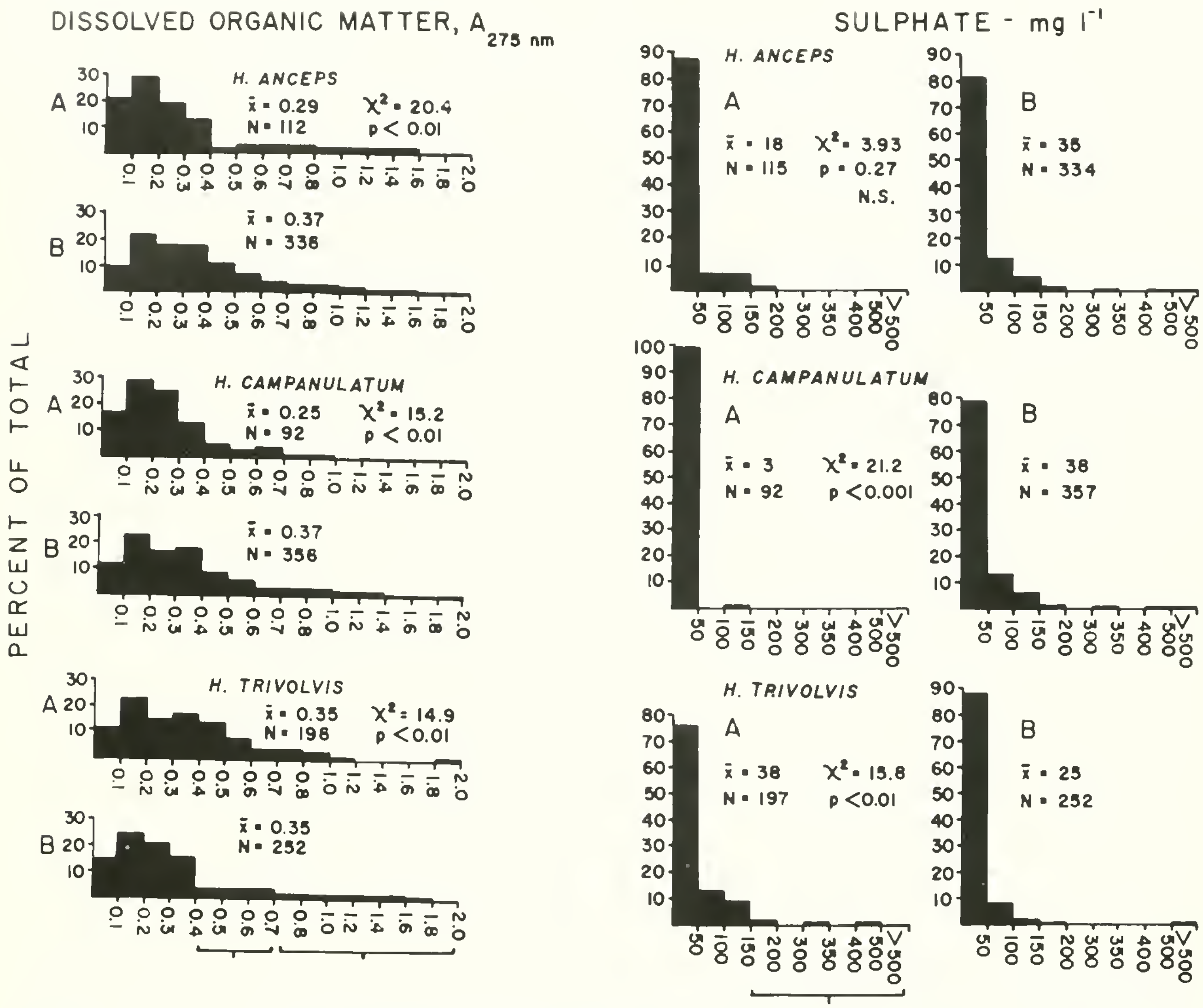

Figure 8. Comparisons of sampling distributions for dissolved organic matter and sulphate of found (A) and remaining (B) sites for the three most frequent species. Horizontal brackets indicate the cells that were combined for chi-square analysis for all species. N.S. = no significant difference.

of habitats that were tolerated by this species was reflected in its comprehensive spatial distribution within the study area. Although it could exist in the Shield-type oligotrophic waters for which *H. campanulatum* was specialized, it could also easily occupy the alkaline and eutrophic habitats that were common in the southwestern portion of the study area and which were beyond the tolerance range limits of the other two species.

Helisoma trivolvis showed the smallest mean HSD value. Thus, if only one *Helisoma* species was present at a site, it was most likely to be *H. trivolvis*. This suggested that it may have been a good colonizer of habitats too severe for the other species, and/or it may have showed a lower rate of extinction, since it would be more likely to survive when environmental fluctuations exceeded the tolerance ranges of the other species.

The negative correlations observed between HSD and several water chemistry parameters, notably sulphate and dissolved organic matter, were due to the fact that all five species could occupy habitats with low water chemistry parameter values, but as the latter increased, progressively fewer species could tolerate them. But, although sulphate, dissolved organic matter, and chloride appeared to be significant, they explained only one-tenth of the variability of HSD. Clearly other environmental factors, as well as elements such as chance associated with dispersal, colonization, and extinction (*e.g.*, Aho, 1978), played important roles.

While many sites could accommodate more than one *Helisoma* species, such instances arose in habitats whose environmental properties fell in the regions of overlap between the tolerance ranges of the different species. Although none of the three most frequent species were positively associated with each other, neither did any

Table 6. Intercorrelations between water chemistry parameters and HSD at the study sites. N = 446–479. Upper diagonal = r, lower diagonal = p. UT = untransformed variables, T = both variables (except pH) log transformed.

	pH	Total dissolved solids	Total alkalinity	Molybdenum reactive phosphorus	Nitrate and nitrite	Chloride	Sulphate	Dissolved organic matter	HSD UT	HSD T
pH	x	0.36	0.32	0.17	0.34	0.30	0.15	−0.34	0.05	0.04
Total dissolved solids	< 0.001*	x	0.47	0.26	0.39	0.66	0.61	0.10	−0.12	−0.21
Total alkalinity	< 0.001*	< 0.001*	x	0.41	0.50	0.39	0.15	0.07	−0.09	−0.08
Molybdenum reactive phosphorus	< 0.001*	< 0.001*	< 0.001*	x	0.21	0.22	0.05	0.13	−0.05	−0.03
Nitrate and nitrite	< 0.001*	< 0.001*	< 0.001*	< 0.001*	x	0.21	0.29	0.02	−0.06	−0.12
Chloride	< 0.001*	< 0.001*	< 0.001*	< 0.001*	< 0.001*	x	0.61	−0.02	−0.11	−0.08
Sulphate	0.001*	< 0.001*	0.001*	0.14	< 0.001*	< 0.001*	x	0.04	−0.07	−0.23
Dissolved organic matter	< 0.001*	0.017*	0.08	0.004*	0.33	0.30	0.22	x	−0.16	−0.18
HSD UT	0.13	0.006*	0.027*	0.13	0.11	0.007*	0.056	< 0.001*	x	x
HSD T	0.23	< 0.001*	0.08	0.28	0.025*	0.20	< 0.001*	< 0.001*	x	x

* Significant correlation.

species exclude any other, since none were negatively correlated. The lack of significant correlation as a consequence of the observed differences in types of habitats frequented by the respective species may enhance the survival of these species by reducing interspecific competition. The habitats containing the greatest numbers of *Helisoma* species in the present study were typically highly productive sites that were also diverse in terms of other gastropods and aquatic macrophytes. A greater variety of microhabitats was available at such sites, allowing for possible niche partitioning of the type described, for example, by Pip and Stewart (1976).

It should be pointed out that, although the tolerance ranges and other characteristics of the species have been examined here for the study area as a whole, individual species may show some regional differences, depending on environmental characteristics. For example Pip (1985) reported that *H. campanulatum* tended to show a narrower ecological tolerance range for total dissolved solids that was concentrated towards the lower end of the concentration scale when only Precambrian Shield sites were considered, compared to the study area as a whole. Such differences, which reflect local environmental conditions, are apparently the result of adaptation.

While the present study was concerned largely with ecological relationships within the genus *Helisoma* in the study area, certain other gastropods as well as aquatic macrophytes may be associated with individual species of this genus. These have been reported elsewhere (Pip, 1978, 1985).

The status of the two rare species, *H. corpulentum* and *H. pilsbryi infracarinatum*, within the ecological framework of the three common species is more difficult to interpret. Both of these taxa appeared to be most frequent in eastern portions of the study area, although both also showed patchy occurrences west of the Shield. From the few recorded cases available, *H. corpulentum* appeared to be a species of oligotrophic waters, with ecological tolerance ranges restricted to low water chemistry parameter values. It was most similar in its physical and chemical ecological attributes to *H. campanulatum,* with which it was positively associated. Its distribution and rarity are perplexing. In the eastern portion of the study area it was apparently limited to the Winnipeg River and was not found in the numerous adjacent lakes and rivers in the region, even though water chemistry parameters of many of these fell within the observed tolerance ranges of this species. The supposition that it may dislike lacustrine habitats is invalidated by its abundance in Whitefish Lake in western Manitoba.

Helisoma p. infracarinatum occurred more frequently than *H. corpulentum*. The observed ecological tolerance ranges for *H. p. infracarinatum* seemed to be intermediate between those of *H. campanulatum* and *H. anceps* for a number of water chemistry parameters (see Pip, 1986). However, it is interesting that, despite the ecological similarity of *H. p. infracarinatum* to the latter two species, it was significantly associated with *H. trivolvis*. This association was seen primarily in the eastern portion of the study area; it remained apparent when a subset of exclusively Precambrian Shield sites was examined (Pip, 1985). In the study area as a whole, *H. trivolvis* was present in > 85% of the cases where *H. p. infracarinatum* was recorded.

The systematic relationship between *H. trivolvis* and

H. p. infracarinatum is unclear. Previous workers (*e.g.*, Baker, 1928, 1936; Clarke, 1973) have remarked on the problematic amount of variation in morphology of *H. p. infracarinatum*. In the present study, many occurrences could be clearly assigned to either *H. trivolvis* or *H. p. infracarinatum*, but at several sites both forms were present together with intergrades. Baker (1928) also reported such intergradation from Wisconsin. The two taxa may possibly be more closely related than is thought at present. One possibility, suggested by Clarke (1973), is that, if the two taxa are interrelated, *H. p. infracarinatum* might be a hybrid of *H. trivolvis* and *H. corpulentum*, although it was much more common in the present study area than *H. corpulentum*. This could be explained by its wider ecological tolerance ranges. Another possibility might be that it is indeed a separate species, and the intergrades observed at some sites may be hybrids between it and *H. trivolvis*. *Helisoma p. infracarinatum* might also be a genetic variant of *H. trivolvis*; populations where the two forms appear to be distinct could be examples of dimorphism. Since, in the study area, *H. p. infracarinatum* showed a well-defined range of ecological parameters within which it occurred, it might be an ecophenotype of *H. trivolvis*, manifested by certain genotypes in the population. Whatever the explanation, it must account for the high degree of association between the two taxa. Until more studies are made, the status of *H. p. infracarinatum* remains uncertain.

LITERATURE CITED

Aho, J. 1978. Freshwater snail populations and the equilibrium theory of island biogeography. II. Relative importance of chemical and spatial variables. Annales Zoologici Fennici 15:155–164.

American Public Health Association. 1971. Standard methods for the examination of water and wastewater. American Public Health Association, New York, 874 p.

Baker, F. C. 1928. The fresh water Mollusca of Wisconsin. Part I. Gastropoda. Bulletin No. 70, Wisconsin Geological and Natural History Survey, Madison, Wisconsin, 507 p.

Baker, F. C. 1932. New species and varieties of *Helisoma* and *Gyraulus* from Canada. The Nautilus 46:6–9.

Baker, F. C. 1936. The freshwater mollusc *Helisoma corpulentum* and its relatives in Canada. Bulletin No. 79, National Museum of Canada, p. 1–37.

Baker, F. C. 1945. The molluscan family Planorbidae. University of Illinois Press, Urbana, IL, 519 p.

Clarke, A. H. 1973. The freshwater molluscs of the Canadian Interior Basin. Malacologia 13(1–2):1–509.

Clarke, A. H. 1981. The freshwater molluscs of Canada. National Museum of Natural Sciences, Ottawa, Ontario, 446 p.

Pip, E. 1978. A survey of the ecology and composition of submerged aquatic snail-plant communities. Canadian Journal of Zoology 56:2263–2279.

Pip, E. 1985. The ecology of freshwater gastropods on the southwestern edge of the Precambrian Shield. Canadian Field-Naturalist 99:76–85.

Pip, E. 1986. The ecology of freshwater gastropods in the central Canadian region. The Nautilus 100:56–66.

Pip, E. and J. M. Stewart. 1976. The dynamics of two aquatic plant-snail associations. Canadian Journal of Zoology 54:1192–1205.

Winer, B. J. 1971. Statistical principles in experimental design. McGraw-Hill, New York, 907 p.

The Publication Date of *Solarium architae* O. G. Costa

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Recent and current interest in the gastropod family Architectonicidae continues unabated with revisions of genera (Bieler, 1984a, 1985a,b, 1986), descriptions of new species (Bieler, 1984b; Merrill & Boss, 1984; Bieler *et al.*, 1985), considerations of the radular apparatus (Bandel, 1984; Boss & Merrill, 1984), the larval shell (Scheltema & Williams, 1983; Bandel *et al.*, 1984), and the anatomy (Haszprunar, 1985a,b) as well as remarks on the geological occurrences (Janssen, 1984; Moroni & Ruggieri, 1984) and zoogeographical ranges (Emerson, 1983; Bieler, 1984a; Melone & Taviani, 1985).

It is troublesome to note that conflicting opinion characterizes the citation of the original publication and date of the binomen *Solarium architae* O. G. Costa, a species of architectonicid. With a distribution in the Atlantic Ocean and Mediterranean Sea (Merrill, 1970), this reasonably common, off shore benthic species has been recently placed in the genus *Pseudotorinia* (Bieler, 1985b; Bieler *et al.*, 1985). The type-specimen in the Zoological Museum of the University of Naples was destroyed during World War II (Bieler, 1985b; Melone & Taviani, 1985).

Dates given for the original introduction of this taxon in the literature include 1830, 1831, 1839, 1841, 1843, and 1844. These include, chronologically arranged: for 1830, Costa (1841), Aradas and Benoit (1870), Monterosato (1873), Jeffreys (1885), Locard (1886), Kobelt (1887), Marshall (1887), Watson (1897), Locard (1899), Tomlin and Shackleford (1914), Bayer (1948), Marche-Marchad (1969), Merrill (1970), Turolla (1974), Piani (1980), Terreni (1981), Micali and Giovine (1983), Boss and Merrill (1984), and Bieler (1985b); for 1831, Ghisotti (1974); for 1839, Ghisotti (1976), Ghisotti and Turolla (1976), and Melone and Taviani (1985); for 1841, Monterosato (1872), Nobre (1938–40), Priolo (1955), and Bieler *et al.* (1985); for 1843, Ghisotti (1974); and for 1844, Hanley (1863), Keen (1971), Abbott (1974), and Sherborn (1923).

The title of the publication in which the binomen supposedly appeared for the first time also differs: *Catalogo de' Testacei viventi nel Golfo di Taranto* (Costa, 1841), *Catalogo dei Testacei viventi nel grande e piccolo mare di Taranto* (Aradas & Benoit, 1870; Parenzan, no date [post 1976]), *Catalogo dei Testacei viventi nel Golfo di Taranto* (Turolla, 1974), *Catalogo de' Testacei viventi nel Piccolo e Grande mare di Taranto* (Ghisotti, 1974) and *Catalogo sistematico dei Testacei viventi nel mare di Taranto* (Ghisotti, 1976).

There are even inconsistencies in quoting the original Latin description (*viz.* Turolla, 1974; Ghisotti & Turolla, 1976).

Thus, the problem of properly citing this species is compounded by conflicting opinion as to the date of publication of the nomen and the title of the original work in which it appeared; the rarity and obscurity of the publications of O. G. Costa further exacerbate this situation.

Oronzio-Gabriele Costa (1787–1867) published numerous papers in conchology and paleontology, a partial list of which was given by Ghisotti (1974). A more complete listing is provided in the Catalogue of Scientific Papers (1800–63), Vol. II, compiled and published by the Royal Society of London (1868). A thorough search of original sources shows that *Solarium architae* was first described and figured in Costa's *Fauna del Regno di Napoli. Animali Molli. Classe III. Gasteropodi, Pettinibranchi*, p. 5, which was published May 12, 1841 (Sherborn, 1910, 1937; Erasmo, 1949; Johnson, 1984). Therein, Costa (1841:6) gave the following citation:

> *Solarium Architae*, Costa, Catal. de' Test. viv. nel Golfo di Taranto (Atti della R. Accad. delle Scienze vol. VI [*sic*].—Rapporto de' lavori della stessa pel 1830, p. 40, n. 15).

This referred to a paper that was in press or preparation in the *Atti* and appeared as:

> Costa, Oronzio-Gabriele. 1844.
> Catalogo de' testacei viventi nel piccolo e grande mare di Taranto redatto sul sistema di Lamarck. Atti della Reale Accademia delle Scienze, Sezione della Società Reale Borbonica, Vol. V, Parte II, pp. 13–66, pls. 1–4.

His comment, "Rapporto de lavori della stessa pel 1830, p. 40, no. 15 [Report of the work of the same title for 1830] must have been construed by subsequent workers as an actually published paper appearing in the *Atti* for

1830. No such paper of that title appears in the *Atti* in 1830 or any year until 1844, nor were any recorded by Sherborn (1922, 1932). This was confirmed by a search of the *Atti* as well as by consulting the *Indice generale dei lavori pubblicata dal MDCCXXXVII al MDCCCCIII* of the *Reale Accademia Delle Scienze Fisiche e Matematiche (Classe della Società Reale di Napoli)* which is an index of *all* published papers in the variously titled series for those dates.

In the 1844 publication of Costa, "*Solarium architae nob.*" appears on p. 48 as the first species of *Solarium* and no figure is included; this dating of the name was cited in Sherborn (1923) and others as noted above.

Although a manuscript of the "Catalogo" or a privately printed paper by Costa may have circulated, much like his rare zoological observations in the Pantellerian Islands (Iredale, 1922), there is no indication of this being the case and no such document has ever been located. Furthermore, authors who cited the year 1830 as the original date for the introduction of *S. architae* either referred to the "Catalogo" in one of its variant titles and/or to the *Atti*, vol. 3, p. 40, no. 15, first so cited by Monterosato (1873).

In summary, *Solarium architae* Costa, despite numerous other datings in the literature, was first described in 1841; the type-specimen is lost; the type-locality is the Gulf of Taranto and the type-figure is the original Costa (1841), pl. 5, figs. a, A, B, C. The species is of particular interest in having such a long lived larval form that its distribution, like a number of teleplanic architectonicids, is amphi-Atlantic.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Abbott, R. Tucker. 1974. American seashells: the marine Mollusca of the Atlantic and Pacific coasts of North America, 2nd ed. Van Nostrand Reinhold Co., New York, 663 p., 24 pls., ca 6000 figs.

Aradas, Andrea and Luigi Benoit. 1870. Conchigliologia [sic] vivente marina della Sicilia e della isole che la circondano. Atti dell'Accademia Gioenia di Scienze Naturali, Catania (3)6:324 p., 5 pls.

Bandel, Klaus. 1984. The radulae of Caribbean and other mesogastropoda and neogastropoda. Zoologische Verhandelingen, Leiden, N. 214, 177 p., 346 text figs., 22 pls.

Bandel, Klaus, Ahuva Almogi-Labin, Christoph Hemleben, and Werner G. Deuser. 1984. The conch of *Limacina* and *Peraclis* (Pteropoda) and a model for the evolution of planktonic gastropods. N. Jb. Geol. Paläont. Abh. 168(1): 87–107, 25 figs., 2 tables.

Bayer, C. 1948. Catalogue of the Solariidae in the Rijksmuseum van Natuurlijke Historie. 3. *Torinia*. Zoologische Verhandelingen, Leiden 4:1–44

Bieler, Rüdiger. 1984a Die Gattungen der Architectonicidae (Gastropoda: "Heterogastropoda"). Allgemeines und Teil 1: *Pseudomalaxis*. Archiv für Molluskenkunde 115(1/3): 53–103, 6 figs., 5 pls.

Bieler, Rüdiger. 1984b. *Heliacus verdensis* n.sp. von den Kapverdischen Inseln (Gastropoda: Architectonicidae). Archiv für Molluskenkunde 115(1/3):105–111, 1 pl.

Bieler, Rüdiger. 1985a. Die Gattungen der Architectonicidae (Gastropoda: "Heterogastropoda"). Teil 2: *Architectonica, Philippia, Dinaxis, Stellaxis, Discotectonica, Solatisonax, Climacopoma, Granosolarium*. Archiv für Molluskenkunde 115(4/6):231–265, 5 pls.

Bieler, Rüdiger. 1985b. Die Gattungen der Architectonicidae (Gastropoda: Allogastropoda). Teil 3: *Pseudotorinia, Nipteraxis, Heliacus, Eosolarium*. Archiv. für Molluskenkunde 116(1/3):89–117, 7 figs., 4 pls.

Bieler, Rüdiger. 1986. Revision of genera in Indo-Pacific species in the family Architectonicidae. American Malacological Bulletin 4(1):108–109.

Bieler, Rüdiger, Arthur S. Merrill, and Kenneth J. Boss. 1985. *Pseudotorinia bullisi*, new species (Gastropoda: Architectonicidae) from subtropical Western Atlantic. The Nautilus 99(4):139–141.

Boss, Kenneth J. and Arthur S. Merrill. 1984. Radular configuration and the taxonomic hierarchy in the Architectonicidae (Gastropoda). Occasional Papers on Mollusks, Harvard University 4(66):349–411, pls. 47–68.

Costa, Oronzio-Gabriele. 1841 (May 12). Fauna del Regno di Napoli. Animali Molli. Classe III. Gasteropodi, Pettinibranchi, Famiglia I, Trocoidei, genera *Solarium, Trochus*. Napoli, Pl. 1 [5], signature 7, p. 1–8.

Costa, Oronzio-Gabriele. 1844. Catalogo de' testacei viventi nel piccolo e grande mare di Taranto redatto sul sistema di Lamarck. Atti della Reale Accademia delle Scienze, Sezione della Società Reale Borbonica 5(2):13–66, 4 pls.

Emerson, William K. 1983. New records of prosobranch gastropods from Pacific Panama. The Nautilus 97(4):119–123.

Erasmo, Geremia D'. 1949. Le date di pubblicazione della "Fauna del Regno di Napoli", di Oronzio-Gabriele Costa e di Achille Costa. Rendiconto dell' Accademia delle Scienze Fisiche e Mathematiche, Napoli, series 4, 16:14–36.

Ghisotti, Fernando. 1974. Malacologi Italiani Illustri. Oronzio-Gabriele Costa. Conchiglie 10(7–8):1–11

Ghisotti, Fernando. 1976. Schede Malacologiche del Mediterraneo. Indice bibliografico, Milano, 4 unnumbered pages.

Ghisotti, Fernando and Giampaolo Turolla. 1976. *Heliacus architae* (O. G. Costa 1839). *In:* Schede Malacologiche del Mediterraneo. Milano, 6 unnumbered pages, 2 figs., map.

Hanley, Sylvanus. 1863. Monograph of the recent species of the genus *Solarium* of Lamarck. *In:* Sowerby, G. B. (ed.). Thesaurus Conchyliorum, or Monographs of genera of

shells 3(1866):227–248, pls. 250–254 [part XXII, *Solarium* (1863), pls. 1–4].

Haszprunar, Gerhard. 1985a. Zur Anatomie und systematischen Stellung der Architectonicidae (Mollusca, Allogastropoda). Zoologica Scripta 14(1):25–43.

Haszprunar, Gerhard. 1985b. The Heterobranchia—a new concept of the phylogeny of the higher Gastropoda. Zeitschrift für Zoologische Systematik und Evolutionshforschung 23(1):15–37.

Iredale, Tom. 1922. Book notes. Proceedings of the Malacological Society of London 15:78–92.

Janssen, A. W. 1984. Mollusken uit het Mioceen van Winterswijk-Miste. Koninklijke Nederlandse Natuurhistorische Vereniging 36:1–451, 82 pls.

Jeffreys, J. Gwyn. 1885. On the Mollusca procured during the "Lightning" and "Porcupine" expeditions, 1868–70 (Part IX). Proceedings of the Scientific Meetings of the Zoological Society of London for the Year 1885, p. 27–63, pls. 4–6.

Johnson, Richard I. 1984. Dates of publication of the molluscan portion (including the Brachiopoda) of the "Fauna del Regno di Napoli" (1829–1886) by Oronzio-Gabriele Costa and Achille Costa. Occasional Papers on Mollusks, Harvard University 4(64):330–332.

Keen, A. Myra. 1971. Sea shells of tropical West America—marine mollusks from Baja California to Peru, 2nd ed. Stanford University Press, California, p. i–xiv, 1–1064, text figs., 22 pls.

Kobelt, Wilhelm. 1886–87. Prodromus faunae molluscorum testaceorum maria europaea inhabitantium. Bauer and Raspe, Nürnberg, p. iv, 1–505.

Locard, Arnould. 1886. Catalogue général des Mollusques vivants de France. Mollusques marins. Paris, 778 p.

Locard, Arnould. 1899. Les coquilles marines au large des côtes de France. Librairie J.-B. Bailliere et Fils, Paris, 198 p.

Marche-Marchad, I. 1969. Les Architectonicidae (Gastropodes Prosobranches) de la côte occidentale d'Afrique. Bulletin de l'Institut française d'Afrique noire (A)31(1): 461–486, 10 pls.

Marshall, William B. 1887. Monograph of the family Solariidae. *In:* Tryon, G. W. (ed.). Manual of conchology: structural and systematic, with illustrations of the species. Philadelphia, 9:3–32, pls. 1–6.

Melone, Giulio and Marco Taviani. 1985. Revisione delle Architectonicidae del Mediterraneo. Lavori della Società Italiana di Malacologia 21(1984):149–192, 67 figs. (Atti del Simposio: Sistematica dei Prosobranchia del Mediterraneo, Bologna, 24–26 Settembre 1982.)

Merrill, Arthur S. 1970. The family Architectonicidae (Gastropoda: Mollusca) in the Western and Eastern Atlantic. Unpublished Ph.D. dissertation, University of Delaware, 338 p., 42 pls. [Microfilm or xerox copy Univ. Microfilms, Ann Arbor, Michigan (No. 71-6444).]

Merrill, Arthur S. and Kenneth J. Boss. 1984. Notes on *Acutitectonica* (Architectonicidae; Gastropoda) with a description of a new species. Occasional Papers on Mollusks, Harvard University 4(65):333–347.

Micali, Pasquale and Ferdinando Giovine. 1983. Elenco dei molluschi rinvenuti nello Stretto di Messina. Comune di Messina, Associazione Malacologica Messinese. 4th Mostra Malacologica Messinese, 18 unnumbered pages.

Monterosato, Tommaso Alleri di. 1872. Notizie intorno alle conchiglie mediterranee. Amento, Palermo, 61 p.

Monterosato, Tommaso Alleri di. 1873. Notizie intorno ai Solarii del Mediterraneo. Amento, Palermo, 11 p., 1 pl.

Moroni, Maria Antonietta and Giuliano Ruggieri. 1984. Uno *Pseudomalaxis* (Gastropoda, Architectonicidae) del Miocene superiore (Saheliano) della Sicilia. Bollettino Malacologico (Milano) 20(9, 12):283–288.

Nobre, Augusto. 1938–40. Fauna malacologica de Portugal. I. Moluscos marinhos e das aguas salobras. 808 p., 87 figs., 49 pls.

Parenzan, Pietro. No date [post 1976]. Carta d'identità delle conchiglie del Mediterraneo. Bibliografia. Bios Taras Editrice, Tarento, 50 p.

Piani, Piero. 1980. Catalogo dei molluschi conchiferi viventi nel Mediterraneo. Bollettino Malacologico (Milano) 16(5): 113–224.

Priolo, Ottavio. 1955. Nuova revisione delle conchiglie marine di Sicilia. Atti della Accademia Gioenia di Scienze Naturali in Catania, 6th series, 10:215–257, pl. 4.

Scheltema, Rudolf S. and Isabelle P. Williams. 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and Western Pacific Mollusks. Bulletin of Marine Science 33(3):545–565.

Sherborn, Charles Davies. 1910. On the dates of publication of Costa's "fauna del Regno di Napoli," 1829–1886. Annals and Magazine of Natural History, London, series 8, 5:132.

Sherborn, Charles Davies. 1922. Index Animalium. British Museum (Natural History), Second Section, Part 1, p. i–cxxxvi, 1–128.

Sherborn, Charles Davies. 1923. Index Animalium. British Museum (Natural History), Second Section, Part 3, p. 385–640.

Sherborn, Charles Davies. 1932. Index Animalium. British Museum (Natural History), Second Section, Part 29, p. cxxxii–cxlvii, 1–208.

Sherborn, Charles Davies. 1937. On the dates of publication of Costa (O. G.) and (A.) Fauna del Regno di Napoli, 1829–1886. Journal of the Society for the Bibliography of Natural History 1(2):35–47.

Terreni, Giuliano. 1981. Molluschi Conchiferi del Mare Antistante la Costa Toscana (Gastropoda, Scaphopoda, Amphineura, Bivalvia, Cephalopoda). Ricerca a cura del Centro Studi sulla Pesca e del Museo di Storia Naturale della Provincia di Livorne, Livorne, 100 p., 10 pls.

Tomlin, J. R. le Brockton and L. J. Shackleford. 1914–15. The marine mollusca of São Thomé, I. Journal of Conchology 14:239–256, 267–276.

Turolla, Giampaolo. 1974. Sul ritrovamento in Adriatico di *Heliacus architae* (O. G. Costa, 1830). Conchiglie 10(9–10):193–198, 2 figs.

Watson, Robert Boog. 1897. On the marine mollusca of Madeira; with descriptions of thirty-five new species, and an index-list of all the known sea-dwelling species of that island. Journal of the Linnean Society of London (Zoology) 26: 233–329, pls. 19, 20.

The Status of *Tritonium viridulum* Fabricius, 1780

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In the last issue of this journal, an article (Sneli and Stokland, 1986:121–124) was published on the taxonomic status of *Tritonium viridulum* Fabricius, 1780. That article contained a number of errors of fact and omission which we feel should be pointed out immediately to prevent additional confusion about the taxon involved.

Sneli and Stokland (1986:121–122) cite Dall's (1887) claim that the holotype of *Tritonium viridulum* Fabricius was a *Bela*. They further quote Dall as saying that *Defrancia viridula* Möller, 1842, was founded on the same specimen. Later in their article, Sneli and Stokland (p. 122, 123) treat *Tritonium viridulum* Fabricius and "*Defrancia viridula* Möller" as two distinct taxa. As pointed out by Pilsbry (1938:116), Möller did not describe a new taxon as *Defrancia viridula*, but simply transferred what he considered to be *Tritonium viridulum* Fabricius to the genus *Defrancia*. This is very clear in Möller (1842:87). The "type lots" of "*Defrancia viridula* Möller", referred to by Sneli and Stokland (1986:122, 123) are not types, but represent what Möller considered to be "*Defrancia viridula* (Fabricius)". For additional discussion on nomenclatural problems involving the misidentification by Möller, see Pilsbry (1938).

Sneli and Stokland mention "two dry specimens of Möller's *viridula* from Greenland which are identified to '*Bela viridula* M. Sars' by Mörch. Michael Sars never described any species with this name, but the sample could indicate that Mörch had Möller's species in mind when he claimed to have discovered that this and Fabricius species were founded on the same specimen." While it is true that Michael Sars did not propose the binomen "*Bela viridula*", G. O. Sars (1878) listed, physically described, and illustrated *Admete viridula* Fabricius (on p. 216, pl. 13, fig. 1a) and *Bela viridula* Möller (on p. 235–236, pl. 16, figs. 7, 8). It appears from Sars' text that the latter listing may have been based on specimens identified by Mörch.

Bouchet and Warén (1985:257) declare that "Mörch never mentioned [the supposed coequivalence of *T. viridula* Fabricius and "*Defrancia viridula* Möller"] in any paper and even the last time he used the name *viridula* (1877) shortly before his death, he used it in the accustomed sense." A partial review of Mörch's publications yields the following citations:

1852:101. *Admete viridula* Fabr. (with *A. crispa* Möll. in synonymy).
1857:10. *Cancellaria* (*Admete*) *viridula* Fabr. (with "*Admete crispa* Möll., *C. buccinoides* Couth., *C. couthoyii* [sic] Jay" in synonymy).
1868:30. *Admete viridula* Fabr.
1869:22. *Admete viridula* Fabr. var. *grandis*

All published evidence clearly shows that Mörch's concept of *Admete viridula* Fabricius was exactly the same as that of all authors except Dall, a few later workers who accepted Dall's opinion without question, and the authors of the paper under discussion.

Sneli and Stokland state that "Fabricius' *Tritonium viridulum* seems difficult to identify with any species" and "should, since the holotype is lost, be regarded as a *nomen dubium*." Pilsbry (1938:116) made the comment that "while there are no figures in [Fauna Groenlandica], the description is good, for the time, and the species, as *Admete viridula* (O. Fabr.) is everywhere accepted." In their work on *Admete*, Bouchet and Warén (1985:257) designated a neotype for *Tritonium viridulum* Fabricius, stating that doing so "will make it possible to keep the name which has been used in a single sense in Europe for 200 years". The neotype selected is one of Möller's specimens. *Admete viridula* (Fabricius), as now fixed by the neotype designation, was properly identified by a large number of authors over the past two centuries. For a partial list of correctly identified references to *Admete viridula* (Fabricius), see Harmer (1918:406). In recent years at least two papers have been published, in addition to the cited paper by Bouchet and Warén, treating *Admete viridula* (Fabricius) and identifying it as the species fixed by the neotype designation (Fretter & Graham, 1985; Harasewych and Petit, 1986).

It was also stated by Sneli and Stokland that the oldest name for "*Admete viridula auctt.*" is *Cancellaria buccinoides* Couthouy, 1838, but that that name is a primary homonym of "*Cancellaria buccinoides* W. Wood, 1828". Couthouy's usage is preoccupied, but it is by

Cancellaria buccinoides G. B. Sowerby I, 1832. This binomen was never used by Wood, nor have we found any other reference attributing it to him.

In short, we find Sneli and Stokland's conclusions to be untenable. *Admete viridula* (Fabricius, 1780) is, and has been, a valid, identifiable, and often cited taxon.

LITERATURE CITED

Bouchet, P. and A. Warén. 1985. Revision of the northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). Bollettino Malacologico, Supplemento 1:121–296, figs. 282–723.

Dall, W. H. 1887. Supplementary notes on some species of mollusks of the Bering Sea and vicinity. Proceedings of the U.S. National Museum 9:297–309, pls. 3, 4.

Fabricius, O. 1780. Fauna Groenlandica. Hafnia et Lipsiae, 452 p.

Fretter, V. and A. Graham. 1985. The prosobranch molluscs of Britain and Denmark. Pt. 8—Neogastropoda. Journal of Molluscan Studies, Supplement 15:435–556, figs. 310–376.

Harasewych, M. G. and R. E. Petit. 1986. Notes on the morphology of *Admete viridula* (Gastropoda: Cancellariidae). The Nautilus 100(3):85–91, figs. 1–11.

Harmer, F. W. 1918. The Eocene Mollusca of Great Britain, being supplementary to S. V. Wood's monograph of the Crag Mollusca. Pt. 3. Palaeontographical Society 70(337): 303–461, pls. 33–44.

Möller, H. P. C. 1842. Index Molluscorum Groenlandiae. Naturhistorisk Tidsskrift 4:76–97.

Mörch, O. A. L. 1852. Catalogus Conchyliorum quae reliquit (. . .) de Yoldi. 1. Hafniae, 172 p.

Mörch, O. A. L. 1857. Fortegnelse over Grønlands Bløddyr. *In:* Rink, H. J. Grönland geographisk og statistik beskrivet, p. 75–100 [separate, p. 3–28].

Mörch, O. A. L. 1868. Fauna Molluscorum Islandiae. Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn (11–13):1–43.

Mörch, O. A. L. 1869. Catalogue des Mollusques du Spitzberg. Mémoires de la Société Malacologique de Belgique 4:7–32 [separate, p. 3–28].

Mörch, O. A. L. 1877. Mollusca. *In:* Rink, H. Danish Greenland, its people and its products. S. King, London. p. 435–442.

Pilsbry, H. A. 1938. On the history and status of *Lora* Gistel. The Nautilus 51(4):115–118.

Sars, G. O. 1878. Mollusca regionis arcticae Norvegiae. Brogger, Christiania, 466 p.

Sneli, J.-A. and Ö. Stokland. 1986. On the taxonomical status of *Tritonium viridulum* Fabricius, 1780 (Gastropoda: Cancellariidae). The Nautilus 100(4):121–124, figs. 1–7.

Sowerby, G. B., I. 1832. *In:* Broderip, W. J. and G. B. Sowerby. [Characters and descriptions of new species of Mollusca and Conchifera collected by Mr. Cuming.] Proceedings of the Zoological Society of London 17:50–61.

Wood, W. 1828a. Index Testaceologicus; . . . [third edition of this title, but called "Second Edition, corrected and revised" on title page]. London, p. i–xxii, [+ 1,] 1–212, 38 pls.

Wood, W. 1828b. Supplement to the Index Testaceologicus; or a catalogue of shells, British and foreign. London, p. i–iv, [+ 1,] 1–59, 8 pls.

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Address inquiries to the current president of UNITAS MALACOLOGIA:

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Redescription of *Acteocina recta* and *A. lepta*, Two Species of Cephalaspidean Gastropods from the Western Atlantic

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ABSTRACT

Acteocina recta (Orbigny, 1841) and *A. lepta* Woodring, 1928, both from the Western Atlantic, are redescribed on the basis of type material and other specimens from museums and private collections. *Acteocina recta*, for which a lectotype is designated, is characterized by its generally small (1–2 mm), thin shell, spiral striae, low spire, double-keeled shoulder, and tapered protoconch, indicative of planktotrophic larval development. It ranges from eastern Florida to Texas, and throughout the Caribbean to Brazil. *Acteocina lepta* was originally described as a Plio-Pleistocene fossil from Jamaica. It is thick-shelled and spirally striate, with a low spire, double-keeled shoulder, and bulbous protoconch, indicative of non-planktotrophic larval development; adults are 2–5 mm in length. In the Recent fauna, it ranges from Bermuda and North Carolina to Louisiana, and throughout the Caribbean to Brazil.

INTRODUCTION

In the course of studying collections of Western Atlantic *Acteocina* species, numerous morphotypes have been distinguished. Three of these, *A. canaliculata* (Say, 1826), *A. candei* (Orbigny, 1841), and *A. atrata* Mikkelsen and Mikkelsen, 1984, have already been recognized as valid species (Mikkelsen & Mikkelsen, 1984). Two others, *A. recta* (Orbigny, 1841) and *A. lepta* Woodring, 1928, have often been misidentified in collections, and have frequently been confused with each other. The present paper redescribes the last two species on the basis of type specimens and other live- and dead-collected material, and redefines their geographic distributions.

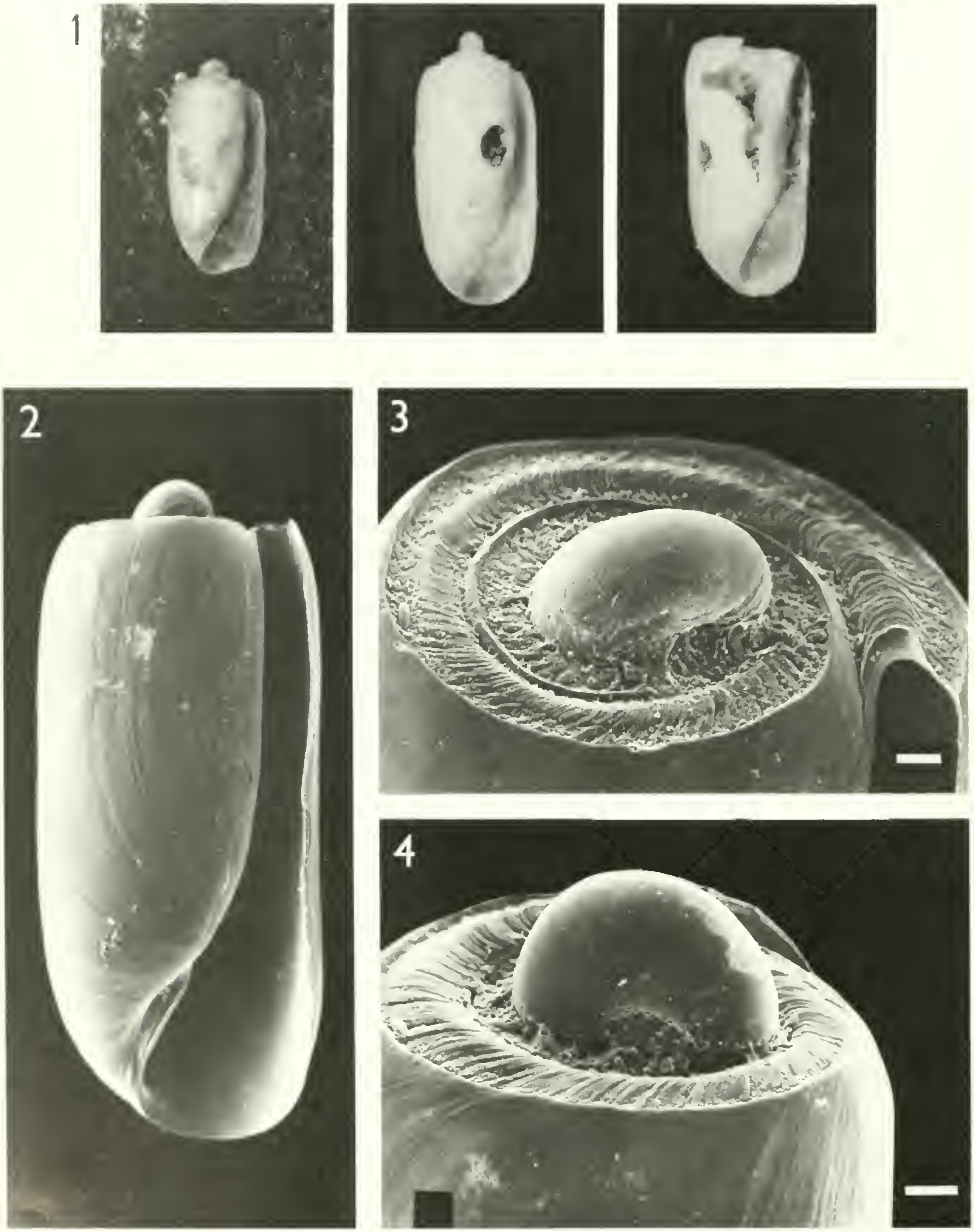
MATERIALS AND METHODS

Dried and wet-preserved specimens from the following museums and private collections were utilized to determine geographic and bathymetric distributions of these species:

ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, PA.
BM(NH), British Museum (Natural History), London.
Coovert Collection, Gary A. Coovert, Dayton, OH.
Edwards Collection, Amy L. Edwards, University of Georgia, Athens, GA.
Finlay Collection, C. John Finlay, Palm Bay, FL.
FSBC I, Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg, FL.
HMNS, Houston Museum of Natural Science, Houston, TX.
IRCZM, Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Ft. Pierce, FL.
Keeler Collection, James H. Keeler, Tallahassee, FL.
Lee Collection, Harry G. Lee, Jacksonville, FL.
LIU, Southampton College (Long Island University), Southampton, NY.
MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA.
MORG, Museu Oceanografico, Rio Grande, Brazil.
Redfern Collection, Colin Redfern, Boca Raton, FL.
UNC-IMS, Institute of Marine Sciences, University of North Carolina, Morehead City, NC.
USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.
Williams Collection, Peggy Williams, Sarasota, FL.
Worsfold Collection, Jack Worsfold, Freeport, Bahamas.

In "Material Examined" sections, an "L" following the number of specimens indicates that at least one of the specimens in the lot was live-collected and contained soft parts; an "E" indicates that all specimens were empty shells.

Shell terminology is after Smith (1967:758–760) and Knight (1952:7–9); radular terminology is after Bertsch (1977:110–111). Radulae and gizzard plates were extracted and prepared for light microscopy using the method previously described (Mikkelsen & Mikkelsen, 1984; Mikkelsen, 1985).



Figures 1–4. *Acteocina recta.* **1.** Syntypes, BM(NH) 1854.10.4.16. Left 1.41 mm (lectotype), center 1.85 mm (paralectotype), right 1.76 mm (paralectotype). **2.** Adult shell from off Ft. Pierce, Florida, 1.62 mm. **3.** Specimen in figure 2, oblique view of

SYSTEMATIC RESULTS

Genus *Acteocina* Gray, 1847

Acteocina recta (Orbigny, 1841) (figures 1–6)

Bulla recta Orbigny, 1841:131; 1842: pl. 4 bis, figs. 17–20.

Material examined: *Syntypes:* 3 specimens [lectotype (1.41 mm), 2 paralectotypes (1.85 mm, 1.76 mm fragment)], BM(NH) 1854.10.4.16. *Other material:* 632 specimens (ANSP, HMNS, LIU, MCZ, MORG, USNM, Worsfold Collection), including the following as representative vouchers: FLORIDA: Off Ft. Pierce: 11L, IRCZM 065:02411, 065:M0063 (microslide with radula and gizzard plates); 2L, USNM 859080; 2L, USNM 859081; 6L, ANSP A11629; 6L, BM(NH) 1986149 (including microslide with radula and gizzard plates).—Bahia Honda Key: 1E, USNM 358296.—LOUISIANA: South Pass: 30E, HMNS 9222.—TEXAS: Southeast of Freeport: 15L, HMNS 8122.—North of Port Isabel: 9E, HMNS 8151.—GREATER ANTILLES: Northwestern Cuba: 1E, USNM 358229.—Cayman Islands: 1E, ANSP 295944.—Haiti: 2E, USNM 859087.—BAHAMAS: North of Abaco: 1E, MCZ 294082.—LESSER ANTILLES: British Virgin Islands: 5L, ANSP 351676.—Antigua: 1E, USNM 859088; 6E, ANSP 8220.—West Grenada: 1E, ANSP 296955.—CENTRAL AMERICA: Belize: 6E, ANSP 285386.—Guatemala: 1E, ANSP 76460.—Panama: 2E, ANSP 200034.—SOUTH AMERICA: South Bahia, off eastern Brazil: 1E, MORG 20.110 (specimen subsequently lost).

Original description: Orbigny (1841:131) originally described *Bulla recta* from the Antilles as "oblong, straight, cylindrical, uniform throughout its length, slender, fragile, shining, displaying nevertheless, under magnification, signs of transverse striations. Spire projecting, very short, strongly channeled at the suture. Aperture linear, straight behind, suddenly enlarging at the front, columella simple, without teeth. Color uniformly white." He distinguished the species by its strongly cylindrical shape and spiral striations, and described its protoconch as "transverse to the spiral axis," or hyperstrophic.

Type material: The type material of *Bulla recta* (figure 1) consists of three specimens, all originally glued to a strip of black paper. The smallest specimen (1.41 mm length), still glued to the paper, has an intact protoconch, highly evident spiral striae, and has retained its transparency. A second specimen (1.85 mm length), although more worn than the first, shows fine spiral striae and a slightly glossy surface. The third specimen (1.76 mm length), consisting of a fragmented body whorl, is of a size and shape to be positively identified as *A. recta*. The latter two specimens are loose, but have glue and paper remnants on their dorsal surfaces. The locality given on the label is "Antilles."

The smallest syntype (figure 1, left), being the best representative of the species-specific characters, is here designated as lectotype for *Acteocina recta*. The remaining two specimens (figure 1, center and right) are designated as paralectotypes.

Diagnosis: Teleoconch thin-walled, cylindrical, with fine spiral striae throughout its length. Shoulder with rounded keel adjacent to suture and sharp keel at shoulder; 2 keels separated by concave trough. Protoconch tapered, indicating planktotrophic development. Lateral radular teeth each with a wing-like expansion bearing a single row of denticles; rachidian teeth with 3 robust denticles per half. Unpaired gizzard plate T-shaped.

Distribution: St. Lucie County, eastern Florida, to southern Texas; Bahamas; Greater and Lesser Antilles; Atlantic Panama; southeastern Brazil. Recorded living at depths of 33–44 m; empty shells collected from 2–128 m.

Description: The orthostrophic, dextral teleoconch of *Acteocina recta* (figure 2) is cylindrical with nearly parallel sides, and has fine spiral striae. Two to three whorls are typical of adult (1–2 mm) specimens. The aperture is narrow (*i.e.*, less than ¼ of the shell width), paralleling the side of the body whorl, and flaring anteriorly. The columella, although "toothless" as Orbigny (1841) stated, bears a single weak fold. The shell walls are thin and transparent in fresh material. The shoulder (figure 3) is double-keeled; a sharp keel at the shoulder is separated from a rounded keel adjacent to the suture by a narrow concave trough of varying depth. The rounded keel and concave trough are crossed by strong axial wrinkles. The spire is nearly flat in specimens under 2 mm; in larger individuals (to 2.5 mm), spire height is typically less than 20% of the shell length. The periostracum is thin and transparent.

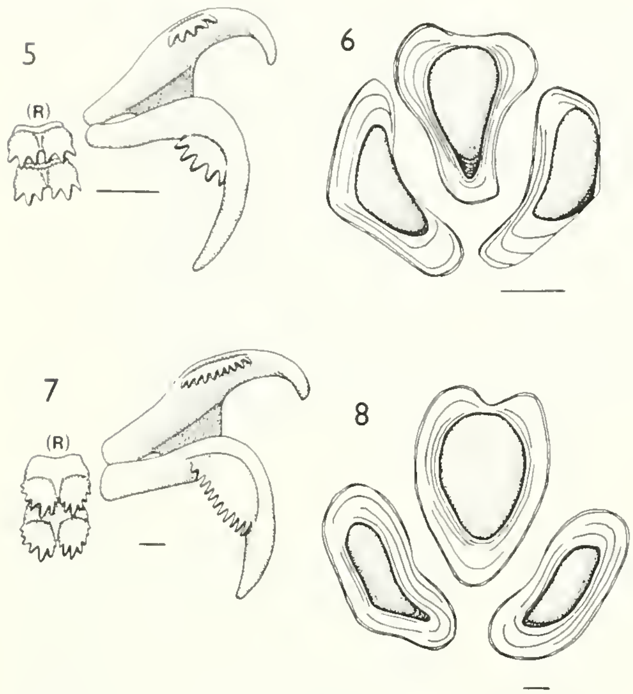
The smooth, hyperstrophic protoconch (figure 4) is tapered and similar in shape to that of *Acteocina canaliculata* (Say, 1826), which was shown to indicate planktotrophic larval development (Mikkelsen & Mikkelsen, 1984: fig. 3, e–g).

The radular formula of *Acteocina recta* is 1-R-1, with 8–14 radular rows in adults (n = 6). The rachidian teeth (figure 5, R) are centrally notched, with each rounded half bearing three (rarely four) sharply pointed, robust denticles. The lateral teeth (figure 5) are sickle-shaped and unicuspid, with the cusp bearing a wing-like expansion supporting one row of 4–6 denticles. A blunt basal tubercle is present for articulation with adjoining lateral teeth.

Three calcareous gizzard plates are present (figure 6): a "pair" of non-identical, but similarly elongated, plates

←

shoulder. Scale bar = 40 μm. **4.** Specimen in figure 2, protoconch showing tapered, planktotrophic-type morphology. Scale bar = 40 μm.



Figures 5–8. Radulae and gizzard plates. *Acteocina recta*: **5.** Two rachidian (R) and two lateral teeth. Scale bar = 10 μm. **6.** Gizzard plates. Scale bar = 100 μm. *A. lepta*: **7.** Two rachidian (R) and two lateral teeth. Scale bar = 10 μm. **8.** Gizzard plates. Scale bar = 100 μm.

opposes a larger "unpaired" plate. The unpaired plate is most dorsal in the crawling animal and is distinctly T-shaped (n = 5).

Remarks: Since its original description, *Acteocina recta* has appeared in the literature mainly as an undiscussed member of various Recent faunal lists (*e.g.*, Gabb, 1873, 1881; Mörch, 1875; Guppy, 1876; Arango y Molina, 1878; Dall, 1889, 1903b; Smith, 1890; Ihering, 1915; Maury, 1922; Johnson, 1934; Lange de Morretes, 1949; Coomans, 1963; Marcus & Marcus, 1964; Abbott, 1974). One such Bermudan record (Peile, 1926) has been found, by examination of voucher specimens (ANSP 141560; see *A. lepta* synonymy), to be *A. lepta*. Pilsbry (1895) and Verrill and Bush (1900) figured *A. recta*, gave brief synonymies, and/or reiterated previous descriptions. In the fossil literature, *A. recta* has been recorded from the Miocene of Santo Domingo (Gabb, 1873; Maury, 1917, 1922), the Oligocene of Jamaica (Dall, 1903a), and the Miocene and Pliocene of Costa Rica (Olsson, 1922, and Gabb, 1881, respectively). None of these previous records, with the exception of Peile (1926), have been verified through specimen examination, although all fall within the verified geographic range of the species.

Some workers (Dall, 1889; Maury, 1917; Olsson, 1922; Woodring, 1928) have cited *Tornatina coixlacryma* Guppy, 1867, from the Jamaican Miocene, as a synonym (in whole or in part) of *Acteocina recta*. However, the neotype of *T. coixlacryma* (USNM 369322, designated by Woodring, 1928) differs markedly from *A. recta* in conchology in having a larger, more robust shell with a deeply channeled suture and bulbous protoconch.

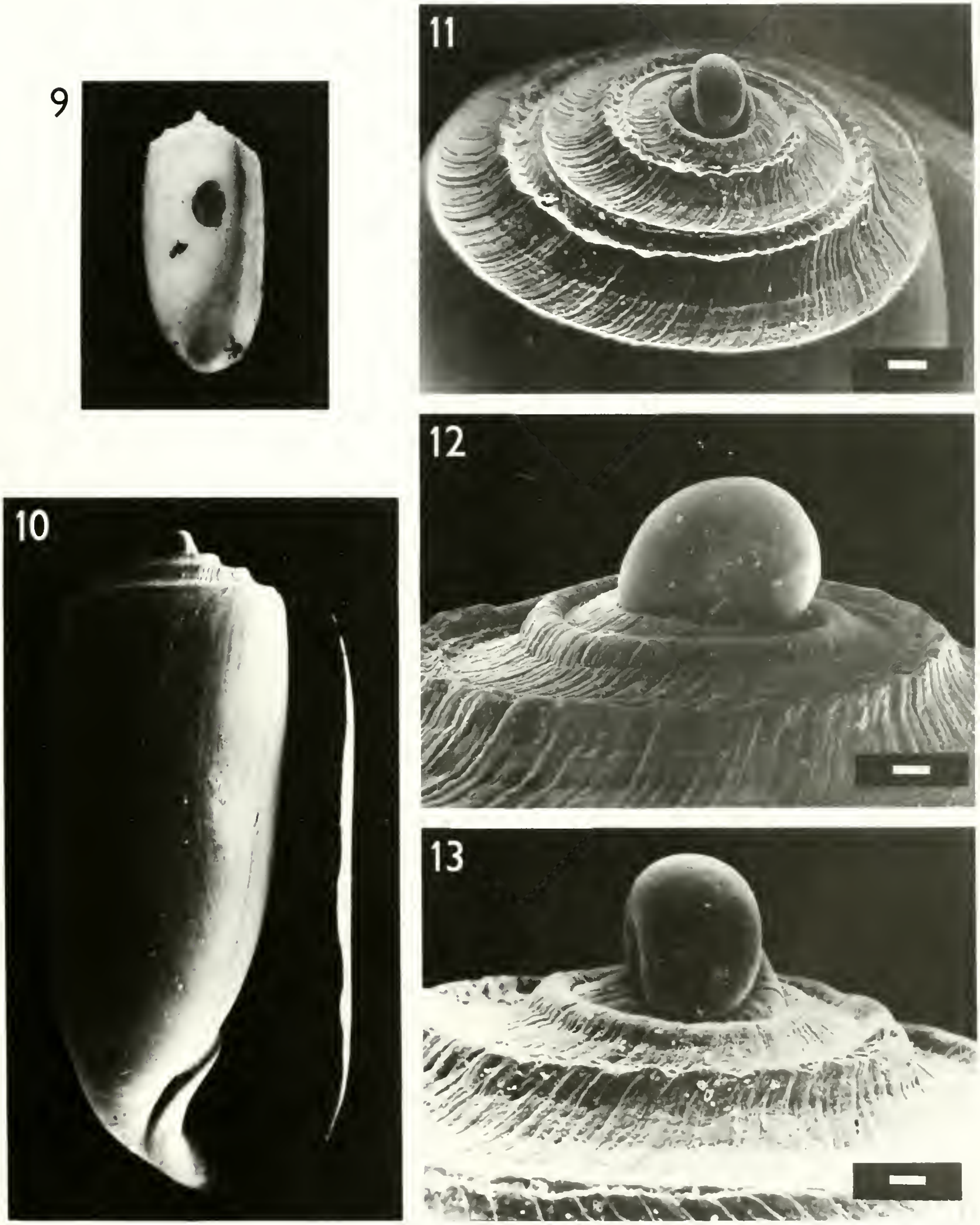
Caution must be used in dealing with small specimens of *Acteocina candei* (Orbigny, 1841), which are often thin-shelled, low-spired and lack distinct subsutural sculptural bands, thus resembling specimens of *A. recta*. The former species may be distinguished in these cases by the absence of spiral striae.

Acteocina lepta Woodring, 1928
(figures 7–13)

Acteocina lepta Woodring, 1928:121, pl. 2, fig. 5.
Retusa candei (Orbigny, 1841). Warmke and Abbott, 1962: 143, pl. 27g; Rice and Kornicker, 1965:129, pl. 8, fig. 10.
Acteocina recta (Orbigny, 1841). Peile, 1926:85 [ref. ANSP 141560 (voucher specimens)].
Tornatina candei (Orbigny, 1841). Rehder, 1981:635, fig. 356.
? *Tornatina cylindrica* Emmons, 1858:181, fig. 182.

Material examined: *Holotype:* 3.78 mm, USNM 369320. Other material: 2,302 specimens (ANSP, FSBC I, HMNS, IRCZM, LIU, MCZ, MORG, UNC-IMS, USNM, and collections of Coovert, Edwards, Finlay, Keeler, Lee, Redfern, Williams, Worsfold) including the following as representative vouchers: Bermuda: 24E, ANSP 141560.—North Carolina: Off Cape Hatteras: 1L, USNM 329930.—Off Cape Lookout: 3L, UNC-IMS 9858.1–3; 2L, IRCZM 065:02056, 065:M0057 (microslide with radula and gizzard plates).—South Carolina: 1E, IRCZM 065:01930.—Georgia: 1E, Edwards Collection.—Florida: Off St. Lucie County: 1E, FSBC I 26258.—Off Palm Beach: 3E, ANSP 359158.—Off Miami: 9E, USNM 859089.—Key Largo: 18E, ANSP 336230.—Key West: 2L, USNM 859090.—Off Sanibel: 1L, MCZ 245062.—Off Tampa: 2E, ANSP 358045.—Off Cape San Blas: 3E, USNM 323422.—Louisiana: Off Cameron: 3E, HMNS 8161.—Greater Antilles: Northern Cuba: 2E, Finlay Collection.—Southeastern Cuba: 1E, USNM 383696.—Jamaica: 27E, USNM 859091.—Cayman Islands: 5E, ANSP 296098.—Dominican Republic: 2E, USNM 807258.—Western Puerto Rico: 1E, USNM 859092.—Bahamas: Greater Abaco Island: 3E, ANSP 357901.—Bimini Islands: 9E, USNM 859093.—Andros Island: 548E, USNM 859094.—Lesser Antilles: Barbados: 2E, USNM 500361.—Central America: Yucatan: 1E, USNM 667674.—South America: Northern Brazil: 8E, MORG 22.365.

Original description: *Acteocina lepta* was originally described as a fossil from Bowden, Jamaica: "shell small, slender, tightly coiled, subcylindrical, body whorl tapering gently at base. Nuclear whorls forming a large tip. Anal fasciole concave, bearing axial puckers, bounded by sharp-edged ridges. Middle of outer lip slightly constricted. Umbilical groove narrow, deep" (Woodring, 1928:121). Although presumed by Woodring to be Late Middle Miocene, Blow (1969) and Robinson and Lamb (1970) have shown the type locality to be Pliocene to Early Pleistocene in age.



Figures 9–13. *Acteocina lepta*. **9.** Holotype, 3.78 mm, USNM 369320. **10.** Adult shell from Cuba, 4.50 mm. **11.** Specimen in figure 10, oblique view of shoulder. Scale bar = 100 μm. **12, 13.** Specimen in figure 10, protoconch showing bulbous, non-planktotrophic morphology. Scale bars = 40 μm.

Type material: The holotype of *Acteocina lepta* (figure 9), although worn, is in generally good condition and has an intact protoconch. A bored hole with worn edges is on the ventral surface of the body whorl. No sculptural details can be discerned on the shell surface, except for distinct axial wrinkles on the shoulder.

Diagnosis: Teleoconch thick-walled, porcellaneous, cylindrical, finely spirally striate throughout its length. Shoulder with rounded, elevated keel adjacent to suture, plus sharp keel at shoulder, separated by a slightly concave, axially wrinkled area. Protoconch well-protruded and bulbous, indicating non-planktotrophic development. Lateral radular teeth each with a wing-like expansion bearing a single row of denticles. Rachidian teeth with robust base, median buttress, and fine denticles. Unpaired gizzard plate heart-shaped.

Distribution: Bermuda; North Carolina to the Florida Keys and to Louisiana; throughout the Caribbean, including the Greater and Lesser Antilles, the Bahamas, Yucatan, and to northern Brazil. Plio-Pleistocene to Recent. Recorded living at depths of 7–226 m; empty shells collected from 2–457 m.

Description: The orthostrophic, dextral teleoconch of *Acteocina lepta* (figure 10) is cylindrical, with nearly parallel sides, and is finely spirally striate. The shells are rather thick, giving a porcellaneous appearance to average-sized (3–5 mm) specimens. The columella bears a single strong fold. In live-collected or fresh-dead material, a thin, light yellow periostracum is evident. The shoulder (figure 11) is sharply keeled, with a second elevated keel just below the suture. Between these keels, the rather wide slope is slightly concave and axially wrinkled. The spire is generally very low, usually 7–9% (maximum 13%) of the total length.

The smooth, hyperstrophic protoconch (figures 12, 13) is typically well-protruded above the first teleoconch whorl. It is bulbous and similar in shape to that of *Acteocina atrata* Mikkelsen and Mikkelsen, 1984 (Mikkelsen & Mikkelsen, 1984: fig. 8, e–g). This type of protoconch has been observed in at least ten species of cephalaspids in the Western Atlantic alone, and is known in two, including *A. atrata*, to reflect capsular metamorphic (= direct) larval development (personal observation). However, some recent workers (Turner *et al.*, 1985) have surmised that prosobranch protoconchs of this same general size and morphology indicate lecithotrophic (= non-feeding planktonic) development. Given this apparent discrepancy, the best we can infer from the available evidence is that *A. lepta* probably has non-planktotrophic development.

The radular formula of *Acteocina lepta* is 1-R-1 with about 16 rows in adult specimens (n = 3). The rachidian teeth (figure 7, R) are centrally notched with each half bearing 6–9 fine, sharply pointed denticles. The base of the rachidian is robust (staining dark pink in acid fuchsin) and extends along the center of the tooth in the form of a triangular buttress. The apex of this buttress meets the approximate center of the indentation between the two halves of the tooth. The lateral teeth (figure 7) are sickle-shaped and unicuspid, with the cusp bearing a wing-like expansion supporting one row of 10–12 denticles. A blunt, basal tubercle is present for articulation with adjoining lateral teeth.

The three subequal calcareous gizzard plates (figure 8) consist of a rounded heart-shaped "unpaired" plate, and two elongated, nonidentical "paired" plates (n = 3).

Remarks: *Acteocina lepta* has been cited in the literature only once since its original description, from the Middle Miocene of Santa Rosa, Veracruz, Mexico (Perrilliat, 1974). It has not been previously recorded as part of any Recent fauna. The results of our previous work on the type species *A. canaliculata* (see Mikkelsen & Mikkelsen, 1984) allow the genus *Acteocina* to be used for this, and other, extant species.

Numerous museum lots of *Acteocina lepta* have been misidentified as *A. recta*. This may stem from a misleading statement by Woodring (1928:121) who originally described *A. lepta* as "the Bowden representative of" and "smaller than" the living *A. recta*.

Acteocina lepta is similar in general appearance to *Tornatina persimilis* Dall, 1895, from the Oligocene of Florida, as noted by Woodring (1928). However, the latter species (holotype, 3.02 mm, USNM 112607) has a tapered, planktotrophic-type protoconch and completely lacks spiral striations.

The original figure of the North Carolina Miocene species *Tornatina cylindrica* Emmons, 1858, is extremely similar to *Acteocina lepta*. A search for type material of Emmon's species has been unsuccessful, making determination of protoconch morphology and other critical features impossible. The original description is inadequate to distinguish it from other species, therefore, *T. cylindrica* must be considered a *nomen dubium*.

Acteocina lepta bears close resemblance to *Tornatina liratispira* E. A. Smith, 1872, the sole conchological difference being protoconch morphology. The four syntypes of the latter species [BM(NH) 1860.5.2.29] were examined; one of the four specimens was found to be *A. candei* (Orbigny). As no live-collected specimens of *T. liratispira* were available for dissection, radular and gizzard plate morphologies remain unknown. Determination of its proper generic placement and relationship with *A. lepta* must therefore await further study. *Tornatina liratispira* is here reported from the Bahamas, the Greater and Lesser Antilles, and the northern coast of Brazil, at depths ranging from 35 to 106 m.

Acteocina lepta has been figured several times in the literature as *A. candei* (Orbigny) (Warmke & Abbott, 1962; Rice & Kornicker, 1965; Rehder, 1981).

DISCUSSION

Morphological characteristics of *Acteocina recta* and *A. lepta* are summarized in table 1.

Extreme caution is advised when identifying specimens of these and other species of *Acteocina sensu lato*. Key characters include shell shape and general sculpture,

Table 1. Distinguishing characteristics of *Actcocina recta* and *A. lepta*.

	A. recta	*A. lepta*
Shell length	1–2 mm	3–5 mm
Shell shape	cylindrical, parallel sides	cylindrical, nearly parallel sides
Spire height	flat to low (<20%)	flat to low (7–13%)
Sutural keel	rounded	sharp, elevated
Trough between shoulder and sutural keels	narrow, concave	wide, concave
Shell walls	thin, transparent	thick, porcellaneous
Columella	weak fold	strong fold
Periostracum	thin, transparent	thin, light yellow
Protoconch	tapered	bulbous
Inferred type of larval development	planktotrophic	non-planktotrophic
Lateral tooth denticles	4–6	10–12
Rachidian tooth denticles	3 per half	6–9 per half
Rachidian buttress	not present	present
Unpaired gizzard plate	T-shaped	heart-shaped

shoulder sculpture, type of protoconch, radula, and gizzard plates. Spiral striae are often exceedingly fine and may be imperceptible in wet (*i.e.*, alcoholic) specimens; momentary drying of the shell surface is frequently necessary for examination. Worn shells, especially those with eroded surfaces and/or missing or worn protoconchs are particularly problematic. All species of *Acteocina* (and other closely related genera) that we have examined thus far are conchologically separable. However, these conchological distinctions may be in the protoconch only. A thorough understanding of species-specific shell characters, in combination with radular and gizzard plate characteristics, is essential.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Company, New York, 663 p., 24 pls.

Arango y Molina, R. 1878. Contribución a la fauna malacologica Cubana. Imp. de G. Montiel y Comp., Habana, 280 text p. + 35 index p.

Bertsch, H. 1977. The Chromodoridinae nudibranchs from the Pacific coast of America. Part I. Investigative methods and supra-specific taxonomy. The Veliger 20(2):107–118.

Blow, W. H. 1969. Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In:* Brönnimann, P. and H. H. Renz (eds.). Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967. E. J. Brill, Leiden, 1:199–421, 54 pls.

Coomans, H. E. 1963. The marine Mollusca of St. Martin, Lesser Antilles, collected by H. J. Krebs. Studies on the Fauna of Curacao and Other Caribbean Islands 16:59–87.

Dall, W. H. 1889. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer "Blake," Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part II. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology at Harvard College 18:1–492, pls. 1–40.

Dall, W. H. 1895. Diagnoses of new Tertiary fossils from the southern United States. Proceedings of the United States National Museum 18(1035):21–46.

Dall, W. H. 1903a. Contributions to the Tertiary fauna of Florida with especial reference to the Silex Beds of Tampa and the Pliocene beds of the Caloosahatchie [*sic*] River . . . Part VI. Concluding the work. Transactions of the Wagner Free Institute of Science of Philadelphia 3:1219–1654, pls. 48–60.

Dall, W. H. 1903b. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species. Reprint, to which are added 21 plates not in the edition of 1889. United States National Museum Bulletin 37, new edition, 232 p., 95 pls.

Emmons, E. 1858. Report of the North Carolina Geological Survey. Agriculture of the eastern counties; together with descriptions of the fossils of the Marl Beds. Bulletins of American Paleontology 56(249):230 p.

Gabb, W. M. 1873. [On the] Topography and geology of Santo Domingo. Transactions of the American Philosophical Society 15:49–259, 2 maps.

Gabb, W. M. 1881. Descriptions of new species of fossils from the Pliocene clay beds between Limon and Moen, Costa Rica, together with notes on previously known species from there and elsewhere in the Caribbean area. Journal of the Academy of Natural Sciences of Philadelphia 8:349–380.

Gray, J. E. 1847. A list of genera of Recent Mollusca, their synonyms and types. Proceedings of the Zoological Society of London, Part 15:129–219.

Guppy, R. J. L. 1867. Notes on West Indian geology, with remarks on the existence of an Atlantis in the Early Tertiary period; and descriptions of some new fossils, from the Caribean [*sic*] Miocene. Geological Magazine 4:496–501.

Guppy, R. J. L. 1876. On the Miocene fossils of Haiti. Quarterly Journal of the Geological Society 32:516–532, pls. 28, 29.

Ihering, H. von. 1915. Die Opisthobranchien der brasilianischen Küste. Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft 47(3):133–144.

Johnson, C. W. 1934. List of the marine Mollusca of the Atlantic coast from Labrador to Texas. Proceedings of the Boston Society of Natural History 40(1):1–204.

Knight, J. B. 1952. Primitive fossil gastropods and their bearing on gastropod classification. Smithsonian Miscellaneous Collections 117(13):1–56, pls. 1, 2.

Lange de Morretes, F. 1949. Ensaio de catalogo dos moluscos do Brasil. Arquivos do Museu Paranaense 7(art. 1):5–216.

Marcus, E. and E. Marcus. 1964. Verzeichnis der euthyneuren Meeresschnecken Brasiliens. Beiträge zur Neotropischen Fauna 3:195–206.

Maury, C. J. 1917. Santo Domingo type sections and fossils. Part I. Bulletins of American Paleontology 5(29):165–415, 39 pls.

Maury, C. J. 1922. Recent Mollusca of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf states. Part 2. Scaphopoda, Gastropoda, Amphineura, Cephalopoda. Bulletins of American Paleontology 9(38):1–142.

Mikkelsen, P. S. 1985. A rapid method for slide mounting of minute radulae, with a bibliography of radula mounting techniques. The Nautilus 99(2–3):62–65.

Mikkelsen, P. S. and P. M. Mikkelsen. 1984. Comparison of *Acteocina canaliculata* (Say, 1826), *A. candei* (d'Orbigny, 1841) and *A. atrata* sp. nov. (Gastropoda: Cephalaspidea). The Veliger 27(2):164–192.

Mörch, O. A. L. 1875. Synopsis molluscorum marinorum Indiarum occidentalium. Malakozoologische Blätter für 1874 und 1875, 22:142–184.

Olsson, A. A. 1922. The Miocene of northern Costa Rica, with notes on its general stratigraphical relations. Part I. Bulletins of American Paleontology 9(39):309 p., 32 pls.

Orbigny, A. d'. 1841. Mollusques, vol. 1. *In:* Sagra, R. Histoire physique, politique, et naturelle de l'Ile de Cuba. Paris, 264 p.

Orbigny, A. d'. 1842. Mollusques, atlas. *In:* Sagra, R. Histoire physique, politique, et naturelle de l'Ile de Cuba. Paris.

Peile, A. J. 1926. The Mollusca of Bermuda. Proceedings of the Malacological Society of London 17(2–3):71–98.

Perrilliat, M. d. C. 1974. Monografía de los moluscos del Mioceno medio de Santa Rosa, Veracruz, México. Parte III. Gasterópodos: Pyramidellidae a Siphonariidae. Universidad Nacional Autónoma de México, Instituto de Geología, Paleontologia Mexicana No. 37:1–46, pls. 1–8, 1 table.

Pilsbry, H. A. 1895. Tectibranchiata. Manual of Conchology 15:181–436, pls. 43–50, 59–61.

Rehder, H. A. 1981. The Audubon Society field guide to North American seashells. Alfred A. Knopf, New York, 894 p.

Rice, W. H. and L. S. Kornicker. 1965. Mollusks from the deeper waters of the northwestern Campeche Bank, Mexico. Publications of the Institute of Marine Science, University of Texas 10:108–172.

Robinson, E. and J. L. Lamb. 1970. Preliminary paleomagnetic data from the Plio-Pleistocene of Jamaica. Nature 227(5264):1236–1237.

Say, T. 1826. Descriptions of marine shells recently discovered on the coast of the United States. Journal of the Academy of Natural Sciences of Philadelphia 5:207–221.

Smith, E. A. 1872. Remarks on several species of Bullidae, with descriptions of some hitherto undescribed forms, and of a new species of *Planaxis*. Annals and Magazine of Natural History 4(9):344–355.

Smith, E. A. 1890. Report of the marine molluscan fauna of the island of St. Helena. Proceedings of the Zoological Society of London [April 1, 1890]:247–319, 4 pls.

Smith, S. T. 1967. The development of *Retusa obtusa* (Montagu) (Gastropoda, Opisthobranchia). Canadian Journal of Zoology 45:737–764.

Turner, R. D., R. A. Lutz, and D. Jablonski. 1985. Modes of molluscan larval development at deep-sea hydrothermal vents. Bulletin of the Biological Society of Washington No. 6:167–184.

Verrill, A. E. and K. J. Bush. 1900. Additions to the marine Mollusca of the Bermudas. Transactions of the Connecticut Academy of Sciences 10:513–544, pls. 63–65.

Warmke, G. and R. T. Abbott. 1962. Caribbean seashells. Dover Publications, New York, xx + 348 p., 44 pls.

Woodring, W. P. 1928. Contributions to the geology and paleontology of the West Indies. Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. Carnegie Institute of Washington, 564 p., 40 pls.

A Revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). II. The New Genera *Hadroconus*, *Rotellenzia*, and *Asthelys*

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ABSTRACT

Three new genera of the superfamily Seguenziacea are proposed. *Hadroconus* is erected for two western Atlantic and one western Pacific species formerly assigned to *Basilissa* Watson, 1879. Another species, *Basilissa lampra* Watson, 1879, is here made type-species of the monotypic genus *Rotellenzia*. One specimen from the syntype series of *Carenzia carinata* (Jeffreys, 1877) from the North Atlantic Ocean is a juvenile of *Basilissa munda* Watson, 1879, which is here established as type-species of *Asthelys* new genus; *Basilissa simplex* Watson, 1879, is also assigned to this genus. Shells of *Hadroconus altus* (Watson, 1879), *Rotellenzia lampra* (Watson, 1879), and *Asthelys munda* (Watson, 1879), are described and illustrated by SEM micrographs and/or light photographs. Comments on utility of shell and radular characters for generic definitions are presented.

INTRODUCTION

The systematics of the Seguenziacea Verrill, 1884, has undergone extensive examination and revision during the last 5 years. Prior to 1983, only six valid genera had been established. An equal number of new genera were erected in 1983 [Marshall, 1983 (5); Quinn, 1983a (1)]. Subsequent research on the western Atlantic fauna has revealed two additional genera, and examination of the unique specimen of *Basilissa lampra* Watson, 1879, makes a third new genus necessary.

In a previous paper (Quinn, 1983b), I noted that shell characters were useful in distinguishing between taxa and, in most cases, were the only characters available at the species and genus levels. For example, differences in size of protoconch, number and distribution of primary and secondary sculptural elements (*e.g.*, spiral carinae, cords, threads, collabral riblets), features of the intersection of the sculptural elements (*e.g.*, nodulose or smooth, sharp or rounded nodules, laterally compressed or not), type of columellar tooth, *etc.*, are important in species discriminations. Some characters, especially shell proportions, may or may not be adequate for species distinctions and must be evaluated on a case-by-case basis.

Ideally, delimitations of genera should entail analyses of shell, radular, and anatomical characters. That ideal is hampered in the Seguenziidae by lack of material available for dissection (see summary in Quinn, 1983b). As a result, all genera have been established principally on the basis of subjective evaluations of shell features, sometimes augmented by a description of the radula. Despite this approach, with the attendant potential for unnecessary generic splitting, authors prior to 1970 were very conservative in erecting new genera. In three recent papers (Marshall, 1983; Quinn, 1983a,b), generic concepts of seguenziids have been refined, again based principally on conchological characters, but no author has presented a discussion of shell characters that, when used in combination, are useful in delimiting genera. I take the opportunity to do so here.

Shell shape: With few exceptions, shell shape gives a good first approximation of generic placement. The following definitions of shell shape will be used in this and subsequent papers: (1) conical—spire height greater than aperture height, sides of spire flat or almost so, sutures not impressed, base flat to weakly convex (*Thelyssa* Bayer, 1971; *Thelyssina* Marshall, 1983; *Basilissa* Watson, 1879; *Hadroconus* new genus; *Asthelys* new genus); (2) depressed conical—similar to (1) but spire height approximately equal to aperture height and base rather strongly convex (*Fluxinella* Marshall, 1983; *Rotellenzia* new genus); (3) conico-turbinate—spire height greater than aperture height, spire weakly to strongly gradate, sutures weakly to strongly impressed, base flat to weakly convex (*Ancistrobasis* Dall, 1889; *Carenzia* Quinn, 1983; *Seguenziella* Marshall, 1983; *Basilissopsis* Dautzenberg and Fischer, 1897; *Seguenziopsis*, Marshall, 1983); (4) ovate-conical—spire height greater than aperture height, sides of spire flat or almost so, sutures weakly impressed, base strongly convex [*Seguenzia* Group III of Quinn, 1983b (this group being described by Marshall, personal

communication)]; and (5) ovate-turbinate—similar to (4) but with spire strongly gradate and sutures often strongly impressed (*Seguenzia* Jeffreys, 1876; *Guttula* Schepman, 1908).

Midwhorl angulation: Presence or absence of a midwhorl angulation is consistent within genera, with one exception (see below). "Midwhorl angulation" includes any angulation that is formed along, although not necessarily confluent with, the anterior (abapical) edge of the posterior labral sinus and is usually weaker than the peripheral carina. Only one genus (*Guttula*) lacks any trace of this angulation at any stage of growth. Among those with an angulation, there are three variations: (1) angulation initially absent, forming on second half of first whorl, then disappearing again later in ontogeny (*Thelyssina* and *Asthelys*); (2) angulation initially present but becoming obsolete or absent after first one to three whorls (*Basilissa*, most *Ancistrobasis*, *Thelyssa*, *Fluxinella*, *Carenzia*, and *Hadroconus*); and (3) angulation present on all whorls, often becoming a strong carina (all other genera, plus *Ancistrobasis regina* Marshall, 1983).

Axial sculpture: Axial sculpture above the periphery usually comprises fine, sharp threads to strong cords tracing, more or less exactly, the outline of the outer lip, but is absent in a few genera. I use the term "sigmoid" to denote the simple reversed S-shape, exemplified by *Ancistrobasis*, and "collabral" for the more complex configuration seen in *Seguenzia* (for general discussion I include both types in the less precise term "axial"). Again, this sculpture falls into several categories: (1) absent on all whorls (*Guttula*, *Fluxinella*, *Thelyssina*, *Seguenziopsis*, and *Asthelys*); (2) initially present on first one or two whorls as sharp, collabral threads, becoming weak, sigmoid threads on subsequent whorls, or disappearing completely except for plications near the sutures, nodulation of the midwhorl angulation, and/or plications on or crenulation of the peripheral carina (*Thelyssa*, *Seguenziella*, *Carenzia*, *Rotellenzia*, and *Hadroconus*); (3) initially present on first one or two whorls as sharp, collabral threads and persisting on all subsequent whorls as strong, rounded, sigmoid cords (*Basilissa*, *Ancistrobasis*, and *Basilissopsis*); and (4) present on all whorls as fine, sharp collabral threads (*Seguenzia* and *Seguenzia* Group III). The axial sculpture may extend onto the base as transverse riblets or threads. The inclination of the axial riblets with respect to the suture line (*i.e.*, an imaginary line connecting the intersections of the riblet ends with the sutures) is useful as an additional character for distinguishing between genera that have similar shell morphologies and sculptural types. At least two cases are known for which this comparison obtains: in *Basilissa* the axials are prosocline, but in *Ancistrobasis* they are opisthocline; in *Thelyssa* the axials are prosocline, but in *Hadroconus* they are opisthocline.

Labral sinuses: The number of labral sinuses in the shell lip is one of the more important characters, if not the most important, in seguenziid systematics. Absence of a sinus in the shell lip does not necessarily reflect a corresponding lack of a sinus in the mantle edge, nor do the shapes of axial riblets necessarily reflect the exact shape of the posterior sinus. Most seguenziid genera have either two or three sinuses (see Marshall, 1983; Quinn, 1983b). *Guttula* alone has none, and *Thelyssina* seemingly has only one. *Seguenzia*, previously defined in part by presence of three sinuses, actually has a fourth (a wide, open, flared extension of the basal lip, rarely preserved in either dead- or live-collected material) located in the extreme inner (adaxial) part of the basal lip; this sinus corresponds to a papillate sinus in the mantle (Quinn, 1983b).

The shape of the posterior sinus has been described as J-, reversed L-, U-, or V-shaped (Quinn, 1983b). However, this actually was a description of the shape of the axial riblets in the selenizone behind the sinus itself. (1) The J- and reversed L-shapes are merely variations on a common theme in which the lower arm of the sinus is essentially parallel to the suture line, and the apex (closed end) is broadly and evenly rounded (*Seguenzia*, *Seguenzia* Group III, *Hadroconus*, and possibly *Thelyssa*). (2) The V-shape is that in which the upper and lower arms of the sinus are divergent and the apex is narrowly rounded (*Carenzia*, *Seguenziella*, *Fluxinella*, *Rotellenzia*). (3) The U-shape should actually, and loosely, be termed "broadly U-shaped", because the apex is very broadly and evenly rounded, but the upper and lower arms of the sinus are divergent, not parallel (*Ancistrobasis*, *Basilissopsis*, *Asthelys*, and probably *Basilissa*). (4) The sinus edge in *Seguenziopsis* apparently sweeps forward in a sigmoid, opisthocline line with the posteriormost point at the suture.

As indicated above, the true shape and depth of the posterior sinus is not necessarily reflected in the shape of the axial sculpture. For example, in *Hadroconus* the sigmoid axial threads suggest a very shallow, broadly U-shaped sinus similar to that of *Ancistrobasis*, but the sinus of the former is actually considerably deeper than that of *Ancistrobasis*, and the lower arm is parallel, or nearly so, to the suture line. However, in *Ancistrobasis*, *Basilissopsis*, and probably *Basilissa*, the sigmoid axials accurately trace the sinus (Marshall, 1983; Quinn, 1983b, unpublished observations). This does not, however, obviate the systematic value of the shapes of axials for discriminating between closely related taxa (Quinn, in preparation).

Depth of the posterior sinus is defined here by arbitrary sinus depth: shell diameter ratios (X)—very shallow = $X < 0.10$; shallow = $0.10 < X < 0.20$; moderate = $0.20 < X < 0.30$; deep = $X > 0.30$.

Umbilicus: The presence, absence, and relative width of the umbilicus may or may not be of systematic significance at the generic level; characteristics of the umbilicus usually are useful only at the species level. However, presence of an umbilical septum is a rare feature in the Seguenziidae, as it also is in the Trochacea. An umbilical septum is known only in *Basilissa superba*

Watson, 1879, and *Thelyssa callisto* Bayer, 1971, and is here considered autapomorphic in both genera.

Radula: The superfamily has been characterized by the presence of a single pair of lateral teeth and more than two pair of marginal teeth in each radular tooth-row (Quinn, 1983b). Including the three new genera defined here, radulae have been illustrated for nine of the fifteen described genera (including *Seguenzia* Group III). These illustrations seem to indicate three distinct types of lateral teeth: (1) Type I is broadly triangular, with the denticulate cusp not narrowed (*Ancistrobasis, Fluxinella, Hadroconus*, and *Guttula* in part); (2) Type II has a broad, triangular base, but with a long, narrow cusp arising from the proximal corner (*Seguenzia, Seguenziella* and *Rotellenzia*); and (3) Type III is a simple, triangular tooth base lacking a cusp (*Guttula* in part, *Carenzia*, and *Seguenzia* Group III). At present, structure of the rhachidian and number of marginals cannot be satisfactorily categorized.

In summary, characters of genus-level importance include shell shape, expression and persistence of a mid-whorl angulation, expression and shape of axial sculpture, shape of the posterior labral sinus, presence or absence of an umbilical septum, and shape of the lateral tooth of the radula. The number of labral sinuses is probably significant at higher taxonomic levels. Features not necessarily useful for discrimination of genera include presence or absence of an umbilicus or columellar tooth and, in most cases, spiral sculpture. However, it must be stressed that all characters must be used in combination, and anatomical characters should also be included when available. I believe that, although anatomical details are lacking for most described genera, and radulae are unknown for several, basing genera principally on shell characters still has validity in the Seguenziidae, and I am confident that anatomical characters, when known, will confirm the validity of most, if not all, seguenziid genera now defined on conchological characters.

Institutional abbreviations used in this paper are: BM(NH), British Museum (Natural History); MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National d'Histoire Naturelle, Paris; TAMU, Systematic Collection of Marine Organisms, Texas A&M University; UMML, Rosenstiel School of Marine and Atmospheric Science, University of Miami; USNM, U.S. National Museum of Natural History.

Hadroconus new genus

Basilissa Watson, 1879:593 (*partim*); 1886:96 (*partim*).—Martens, 1881:56 (*partim*).—Dall, 1881:48; 1885:34 (*partim*); 1889a:32, 384 (*partim*); 1889b:164–165 (*partim*); 1890: 354; 1927:109 (*partim*).—Fischer, 1885:827 (*partim*).—Pilsbry, 1889:15, 419 (*partim*).—Schepman, 1908:61 (*partim*).—Maury, 1922:157 (*partim*).—Thiele, 1929:48 (*partim*).—Johnson, 1934:73 (*partim*).—Wenz, 1938:276 (*partim*).—Cotton, 1959:189 (*partim*).—Keen and Cox, 1960: 1250 (*partim*).—Clarke, 1962:12 (*partim*).—Bayer, 1971: 123.—Abbott, 1974:39 (*partim*).—Quinn, 1979:49 (*partim*); 1981:74 (*partim*); 1983b:729 (*partim*).—Goryachev, 1979:70 (*partim*).—Boss, 1982:974 (*partim*).
Seguenzia: Dall, 1881:48 (*partim*).

Type-species: *Basilissa alta* Watson, 1879; here designated.

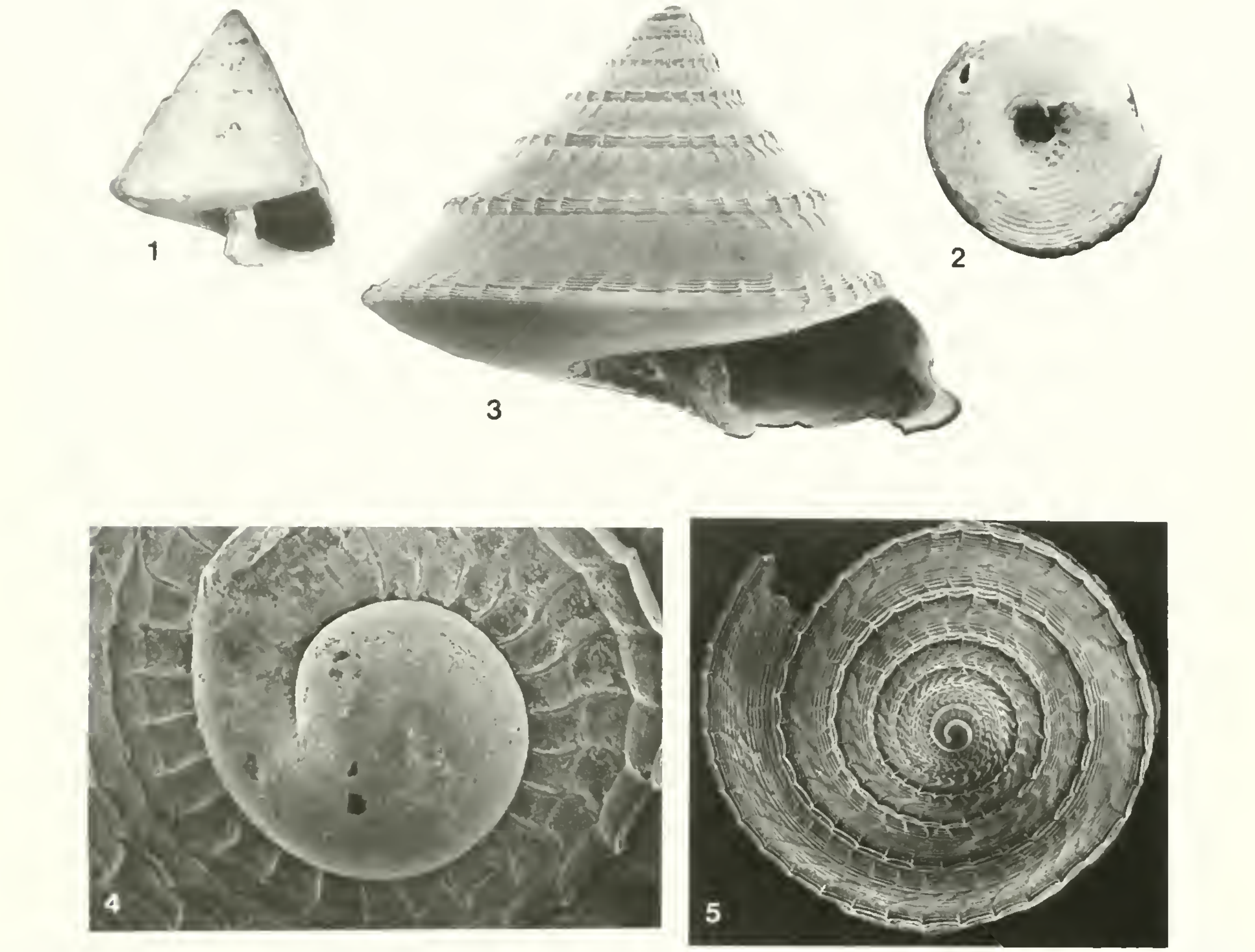
Gender: Masculine.

Diagnosis: Shell small, conical, peripherally carinate, umbilicate, nacreous under thin outer porcelaneous layer, white, polished; spire with flat to slightly concave sides, sculptured by widely spaced, sigmoid axial riblets, and fine spiral threads; periperal carina strong, overlaid with several spiral threads, crenulated by terminations of axial riblets; base slightly convex, with strong, flattened spiral cords and/or narrow threads; umbilicus wide, deep, funnel-shaped, bounded by strong, tuberculate cord; aperture subrectangular; outer lip thin, with shallow posterior sinus occupying adapical half of whorl, claw-like near periphery; basal lip thin, with wide, shallow sinus in outer part; columella straight, slightly oblique, somewhat inflated medially, terminating in a rounded boss.

Remarks: Cossmann (1888) designated *Basilissa superba* Watson, 1879, as type-species of *Basilissa* Watson, 1879, although *B. alta* Watson, 1879, has been the species most frequently associated with that genus. Because that type-designation may not be changed, *Hadroconus* is erected for *B. alta*, *B. sibogae* Schepman, 1908, *B. watsoni* Dall, 1927, and an undescribed western Atlantic species. Together, these four species form a morphologically cohesive species-group that may be distinguished from all other seguenziacean genera. Shells of these four species are small ($<$ 10 mm), have spiral sculpture much weaker than axial riblets, or predominantly absent, the axial riblets are strongly sigmoid and opisthocline, and the umbilicus lacks a septum. Shells of *B. superba* are large ($>$ 20 mm), have spiral sculpture subequal to axial riblets, axial riblets almost a simple prosocyrt arc except for a weak opisthocyrt sinuation near the adapical suture, axials weakly prosocline, and umbilicus partially covered by a septum. In addition, shells of *Hadroconus* species usually have height : width (h:w) ratios less than 1.0, those of *B. superba* greater than 1.0; however, two specimens of *H. altus* (UMML 30.8155) have h:w ratios of 1.03 and 1.07, and Okutani (1982) recorded two juvenile specimens of *B. superba* with h:w ratios of 0.96 and 0.98 (he did not indicate whether apical parts of these specimens are intact).

Shells of *Hadroconus* are most similar to those of *Thelyssa* Bayer, 1971, but differ in that the axial riblets are rather strongly sigmoid and opisthocline, and the umbilical walls lack callus and an umbilical septum. *Hadroconus* and *Thelyssa* are apparently sister taxa separated principally by the autapomorphic umbilical septum of *Thelyssa*.

Although I have not had an opportunity to examine a properly preserved specimen of any species of *Hadroconus*, dried specimens of both *H. altus* and *H. watsoni* were available for study and afforded the following ob-



Figures 1–5. *Hadroconus altus* (Watson, 1879). **1, 2.** Apertural and basal views of lectotype of *Basilissa alta*, BM(NH) 1887.2.9.351, height 6.3 mm, maximum diameter 5.9 mm. **3.** Apertural view of specimen from *Gerda* station G-965, UMML 30.7759 (SEM micrograph, × 9). **4.** Protoconch of another specimen from G-965 (SEM, × 140). **5.** Same, apical view (SEM, × 9).

servations of external anatomy. A well-developed epipodium bears four (or five) to six epipodial tentacles. The mantle edge has two broad sinuses, corresponding to the basal and posterior labral sinuses of the shell; mid-dorsally is a prominent, seemingly papillate tentacle, to the left of which is a narrow, C-shaped sinus which corresponds to the peripheral angulation of the shell. The esophagus, seen by transparency after the animals were soaked in trisodium phosphate, extends posteriorly from the buccal area, sharply turns ventrally at the level of the last intestinal turn, and then runs posteriorly along the ventrolateral surface of the right intestinal tract. The intestine is similar to that of *Seguenzia* sp. *cf. S. eritima* Verrill, 1884 (Quinn, 1983b), but coils in the opposite direction; the shape of the fecal string is also similar to that of *Seguenzia*: oval with a shallow medial groove on one side. The cephalic tentacles are long, papillate, appressed basally, and a long, slender penis arises just to the right of the right cephalic tentacle. On either side of the snout is a prominent, paddle-shaped oral lappet.

Etymology: From the Greek *adros*, stout, strong, and *konos*, a cone.

Hadroconus altus (Watson, 1879)
(figures 1–5)

Basilissa alta Watson, 1879:597; 1886:100, pl. 7, fig. 8.—Martens, 1881:56.—Dall, 1881:48, 1885:34; 1889a:32, 384, 1889b:164–165, 1890:354.—Pilsbry, 1889:419, pl. 36, fig. 5.—Maury, 1922:157.—Johnson, 1934:73.—Cotton, 1959: 189.—Clarke, 1962:12.—Bayer, 1971:123, figs. 6D–G, 7A–D.—Abbott, 1974:37, fig. 239.—Quinn, 1983b:729, figs. 13, 28, 40.

Seguenzia delicatula Dall, 1881:48, 1885:265.

Basilissa alta var. *oxytoma* Watson, 1886:100, pl. 7, fig. 8a.—Pilsbry, 1889:421, pl. 36, fig. 4.

Basilissa alta var. *delicatula*: Dall, 1889a:384, pl. 22, figs. 2, 2a; 1889b:164–165.—Pilsbry, 1889:421, pl. 48, figs. 3, 4.—Maury, 1922:158.

Basilissa delicatula delicatula: Johnson, 1934:73.

Basilissa (*Basilissa*) *alta*: Quinn, 1979:50, figs. 83, 84.

Material examined: 1 specimen, UMML 30.8156; *Columbus Iselin* sta. CI-356, 24°28.3′N, 77°29.5′W, 1,597 m; 40 foot otter trawl; August 20, 1975.—1 specimen, UMML 30.8146; *Gerda* sta. G-478, 24°15′N, 82°11′W, 543–348 m; 10 foot otter trawl; January 26, 1965.—3 specimens, UMML 30.8152; *Gerda* sta. G-967, 24°15′N, 82°26′W, 499–503 m; 10 foot otter trawl; February 2, 1968.—1 specimen, UMML 30.8018; *Gerda* sta. G-1099, 24°12.5′N, 82°50′W, 622 m; 10 foot otter trawl; April 28, 1969.—1 specimen, UMML 30.8144; *Gerda* sta. G-356; 24°11′N, 81°37′W, 672 m; 10 foot otter trawl; September 15, 1964.—1 specimen, UMML 30.8151; *Gerda* sta. G-966, 24°10′N, 82°22′W, 553–558 m; 10 foot otter trawl; February 2, 1968.—1 specimen, UMML 30.8147; *Gerda* sta. G-815, 24°08′N, 79°48′W, 618 m; 10 foot otter trawl; June 27, 1967.—1 specimen, USNM 94941; *Blake* sta. 43, 24°08′N, 82°51′W, 620 m.—1 specimen, UMML 30.8145; *Gerda* sta. G-370, 23°54′N, 81°19′W, 1,281 m; 16 foot otter trawl; September 16, 1964.—1 specimen, UMML 30.7764; 2 specimens, UMML 30.8150; *Gerda* sta. G-964, 23°46′N, 81°51′W, 1,390–1,414 m; 10 foot otter trawl; February 1, 1968.—5 specimens, UMML 30.7759; *Gerda* sta. G-965, 23°45′N, 81°51′W, 1,394–1,399 m; 10 foot otter trawl; February 1, 1968.—1 specimen, UMML 30.8022; *Gerda* sta. G-1112, 23°44′N, 81°14′W, 2,276–2,360 m; 10 foot otter trawl; April 30, 1969.—1 specimen, MCZ 7596; *Blake* sta. 41, 23°42′N, 83°13′W, 1,573 m.—1 specimen, UMML 30.7692; *Gerda* sta. G-963, 23°41′N, 82°16′W, 1,441–1,454 m; 10 foot otter trawl; February 1, 1968.—7 specimens, UMML 30.8149; *Gerda* sta. G-960, 23°30′N, 82°35′W, 1,692–1,697 m; 10 foot otter trawl; January 31, 1968.—5 specimens, UMML 30.8148; *Gerda* sta. G-959, 23°25′N, 82°26′W, 1,830 m; 10 foot otter trawl; January 31, 1968.—6 specimens, MCZ 135024; *Atlantis* sta. 2993, 23°24′N, 80°44′W, 1,061 m; 14 foot Blake trawl; March 15, 1938.—1 specimen, MCZ 135022; *Atlantis* sta. 2987E, 23°19′N, 79°59′W, 576 m; 14 foot Blake trawl; March 13, 1938.—1 specimen, MCZ 135023; *Atlantis* sta. 2988, 23°15′N, 79°57′W, 695 m; 14 foot Blake trawl; March 14, 1938.—1 specimen (lost), MCZ 7598 (? holotype of *Seguenzia delicatula*); 1 specimen, USNM 94943; *Blake* sta. 2, 23°14′N, 82°25′W, 1,472 m.—1 specimen, MCZ 135021; *Atlantis* sta. 2989, 23°10′N, 80°04′W, 658 m; 14 foot Blake trawl; March 14, 1938.—11 specimens, MNHN; *Alaminos* sta. 66-A9-15, 28°13.5′N, 87°04′W, 1,200–800 m; 10 ft midwater trawl; 1967.—Fragments, USNM 93805; *Albatross* sta. 2384, 28°45′00″N, 88°15′30″W, 1,719 m; large beam trawl; March 3, 1885.—3 specimens, MNHN; *Alaminos* sta. 69-A11-7, 27°01.3′N, 94°43.5′W, 1,399 m; 3 m benthic skimmer; 1969.—3 specimens, TAMU 4-1950; *Alaminos* sta. 69-A11-74, 21°29′N, 96°41.5′W, 1,189–1,280 m; 3 m benthic skimmer; August 22, 1969.—1 specimen, UMML 30.8153; *John Elliott Pillsbury* sta. P-585, 21°02′N, 86°29′W, 567–570 m; 10 foot otter trawl; May 23, 1967.—1 specimen, MCZ 135261; *Atlantis* sta. 3370, 20°47′N, 75°11′W, 829 m; 14 foot Blake trawl; April 20, 1939.—1 specimen, USNM 429445; 12 specimens, USNM 429465; 3 specimens, USNM uncatalogued; Johnson-Smithsonian Deep-Sea Expedition sta. 67, 18°30′12″N, 65°45′48″W, 329–512 m; 4 foot dredge; February 23, 1933.—1 specimen, BM(NH) 1887.2.9.351 (lectotype); 1 specimen, BM(NH) 1887.2.9.352 (paralectotype); *Challenger* sta. 24, 18°30′30″N, 65°05′30″W, 713 m; March 25, 1873.—1 specimen, USNM 214142; *Albatross* sta. 2750, 18°30′N, 63°31′W, 913 m; 2 foot ship's dredge; November 27, 1887.—2 specimens, UMML 30.8327; *John Elliott Pillsbury* sta. P-988, 18°29.3′N, 63°24′W, 686–723 m; 5 foot Blake trawl; July 23, 1969.—2 specimens, UMML 30.8328; *John Elliott Pillsbury* sta. P-1255, 17°18′N, 78°32′W, 23–622 m; 10 foot otter trawl; July 14, 1970.—4 specimens, UMML 30.8155; *John Elliott Pillsbury* sta. P-1261, 17°13′N, 77°50′W, 595–824 m; 10 foot otter trawl; July 15, 1970.—14 specimens, USNM 95399; 9 specimens, USNM 614087; *Albatross* sta. 2751, 16°54′N, 63°12′W, 1,257 m; large beam trawl; November 28, 1887.—1 specimen, MCZ 7597; *Blake* sta. 163, 16°03′10″N, 61°52′20″W, 1,407 m; January 20, 1879.—1 specimen, UMML 30.8154; *John Elliott Pillsbury* sta. P-861, 12°42′N, 61°05.5′W, 18–744 m; 10 foot otter trawl; July 4, 1969.—2 specimens, USNM 94942; *Blake* sta. 264, 12°03′15″N, 61°48′30″W, 767 m; March 1, 1879.—1 specimen, USNM 96876; *Albatross* sta. 2754, 11°40′N, 58°33′W, 1,609 m; large beam trawl; December 18, 1887.—Fragments, BM(NH) 1887.2.9.353; *Challenger* sta. 120, 8°37′S, 34°28′W, 1,235 m; September 9, 1873.—11 specimens, USNM 150756; *Albatross* sta. 2760, 12°07′S, 37°17′W, 1,864 m; large beam trawl; December 18, 1887.

Description: Shell small (height of largest specimen 7.2 mm, width 8.2 mm), conical, peripherally carinate, polished, white, iridescent under thin outer porcelaneous layer. Protoconch 375–450 μm (usually about 425 μm) in maximum diameter, prominent, glassy. Teleoconch whorls 7.5–8.0; spire whorls flat, with widely spaced (2–4 per mm) sigmoid axial riblets and fine spiral threads; sculpture usually strongest near suture and periphery, obsolete medially on whorls 3–6, becoming distinct again on whorls 7–8; suture distinct but not impressed. Periphery marked by strong carina, overlain by about 4 spiral threads, rendered strongly denticulate by the axial riblets, visible on all whorls. Base almost flat, often smooth medially, otherwise with strong spiral cords and obscure transverse threads in striae between spiral cords; sculpture stronger near umbilicus. Umbilicus wide, approximately 24% maximum shell diameter, bounded peripherally by strong, tuberculate spiral cord. Aperture subrectangualr, lips thin; outer lip bisinuate, with peripheral spur, and with wide, moderately deep, U-shaped posterior sinus, abapertural edge of which slightly flared; basal lip with wide, shallow, sinus, with weakly flared edges, apex in outer third of lip; columella straight, slightly oblique, distinctly inflated medially, terminating in rounded boss.

Animal occupies approximately 2 whorls, with estimated length of 8–10 mm. Epipodium prominent, flaplike, bearing 4 (probably 5) epipodial tentacles, ante-

riormost and posteriormost rather long, slender, middle 2 (or 3) much shorter. Esophagus running posteriorly from buccal area, making sharp ventral turn at level of last intestinal loop, then running posteriorly along ventral margin of right intestinal tract. Intestine very long, probably 15–20 mm total length when complete, running forward along left side of animal, forming series of tight convolutions and loops in anterior 2–3 mm, abruptly crossing to right side approximately 2 mm posterior to mantle edge, making short, tight dorsal loop before running posteriorly in series of strong sinuations; at some point posterior to preserved sections, intestine makes sharp U-turn, running anteriorly along left side of animal, the 2 sections closely appressed posteriorly, then separated by intervening structures anteriorly; about 3 mm posterior to mantle edge it makes 2 tight right-left loops, then runs straight along left side for about 2 mm, turning sharply right for about 0.5 mm, finally running anteriorly for final 1.5 mm; anus lying just posterior to edge of mantle on right side of animal. A 3 mm long fragment from near posterior reach of intestine contained some loops of intestine and/or esophagus ventrally and an ovate, 1.75 mm long organ that occupied the same relative position as the kidney of *Seguenzia cf.* sp. *S. eritima* (see Quinn, 1983b: fig. 34), but was solid and evenly rounded, rather than delicate and somewhat lobulate as in the *Seguenzia* species. No other features were observed because of poor preservation. Radula lost during preparation for SEM.

"The operculum is circular, very thin, concave, of about four whorls. The radula . . . has a rhachidian with a triangular cusp finely denticulated on the sides, a wide lateral with an inwardly directly [*sic*, directed] triangular cusp denticulated on both sides, and several (6 or 7) marginals, flat and rather narrow, denticulated along most of the outer edge but on the inner edge only near the tip" (Bayer, 1971:124).

Measurements: Lectotype [BM(NH) 1887.2.9.351; here designated]: 6.3 mm high, 5.9+ mm wide. Largest specimen: 7.2 mm high, 8.2 mm wide.

Type-locality: NW of St. Thomas, Virgin Islands, *Challenger* sta. 24, 18°30′30″N, 65°05′30″W, 713 m (here designated).

Remarks: All four species of *Hadroconus* are very similar morphologically. *Hadroconus sibogae* (Schepman, 1908), from Makassar Strait, off Celebes Island, Indonesia, differs from the three western Atlantic species in that it totally lacks spiral sculpture on the upper whorl surface, except for "one or two spiral elevated striae . . . on part of the upper whorls" (Schepman, 1908:62–63). The three western Atlantic species are more difficult to distinguish from each other, especially because of the intraspecific variation of shells of *H. altus*. Discussions and analyses of characters distinguishing *H. altus* from *H. watsoni* (Dall, 1927) and the undescribed species will be presented in a future paper revising the western Atlantic *Hadroconus*.

Intraspecific variation in shells of *H. altus* is extensive. The height : width (h:w) ratio varies from 0.68 to 1.07 ($\bar{x} = 0.85 \pm 0.10$; N = 22); the lower the ratio, the more distinctly concave the spire outline becomes. In a manner similar to that of the spiral sculpture above the periphery, the basal spiral cords tend to become obsolete on the medial part of the base. This smooth area varies from 15% to 47% ($\bar{x}$ = 28.5%) of the umbilicus–periphery distance. In a few specimens [BM(NH) 1887.2.9.351–352, and UMML 30.8018, 30.8151, and 30.8155], the basal spiral cords are all strong and separated by strong grooves. These specimens also had the highest h:w ratios (0.97–1.07) and some of the smallest protoconchs (375–400 μm), but these values were not significantly different from those of the lower spired forms (Student's t; $P < 0.05$).

Hadroconus altus is known from the Bahamas, Straits of Florida, Gulf of Mexico, Yucatan Channel, the entire Antillean Arc, and off Brazil. Bathymetric occurrence is about 500–700 m in the northern Straits of Florida, and generally deeper than 1,000 m elsewhere, with the deepest record (2,276–2,360 m) in the southern Straits of Florida. Depths of the three lots with live-collected specimens were 805–722 m (UMML 30.8328, P-1255), 1,200–800 m (MNHN, *Alaminos* sta. 66-A9-15), and 1,390–1,414 m (UMML 30.8150, G-964). *Hadroconus altus* thus seems to inhabit depths considerably greater than those in which either of the other western Atlantic species live (*H. watsoni*: approximately 430–805 m: *Hadroconus* n. sp.: 329–512 m; personal observations).

Rotellenzia new genus

Basilissa: Watson, 1879:593 (*partim*); 1886:96 (*partim*).—Schepman, 1908:61 (*partim*).—Cotton, 1959:189 (*partim*).

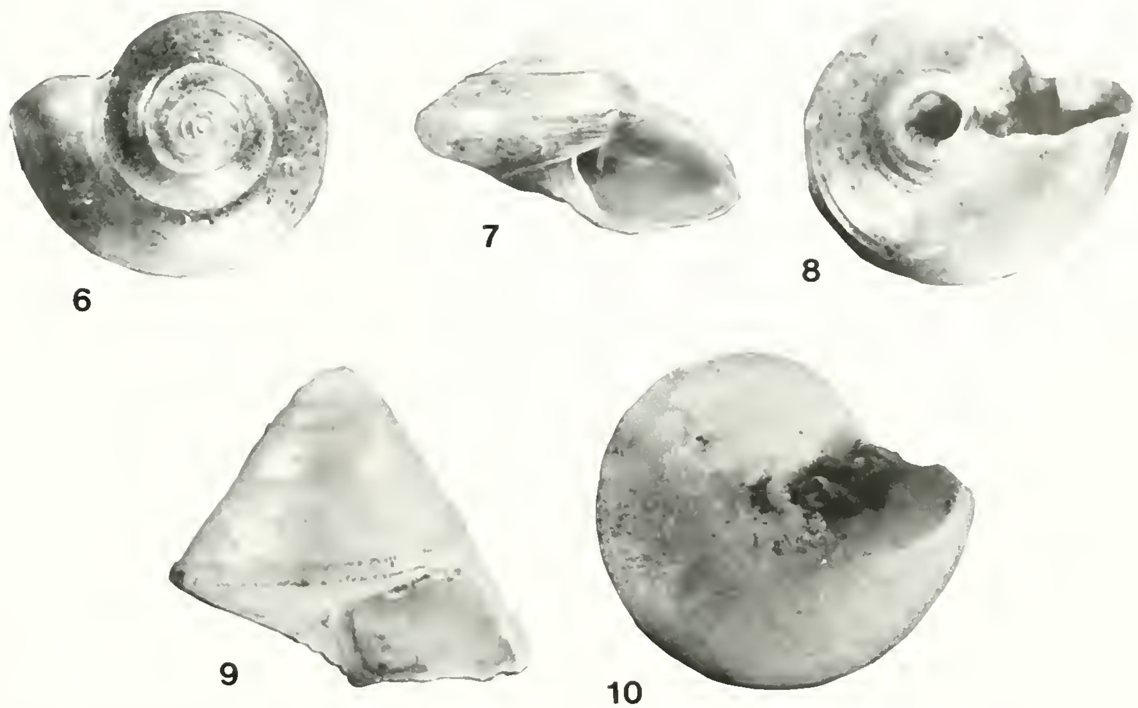
Seguenzia Group II: Quinn, 1983b:728 (*partim*).

Type-species: *Basilissa lampra* Watson, 1879; here designated.

Gender: Feminine.

Diagnosis: Shell of moderate size, depressed conical, weakly carinate peripherally, fragile, brilliantly iridescent under very thin outer porcelaneous layer, color brassy; spire almost flat-sided, sutures weakly impressed; whorls with 2 weak carinae at periphery, visible only on last whorl, with numerous spiral threads above peripheral cords, strongest on first 3 whorls, obscure subsequently; axial sculpture of low riblets on first 1.5 whorls, thereafter almost absent; base weakly convex, with numerous spiral threads, umbilicate; umbilicus wide, defined by strong, smooth spiral cord; aperture rhomboidal; lips thin with broad, V-shaped posterior sinus, and broad, very shallow, U-shaped basal sinus; anterolateral sinus, if present, probably narrow, shallow and U-shaped; columella thin, very weakly sigmoid, edentate.

Remarks: The shell of the type-species of this genus is most similar to those of species of *Seguenziella* Marshall, 1983. *Rotellenzia lampra*, however, lacks the strong midwhorl and peripheral carinae which characterize *Se-*



Figures 6–8. *Rotellenzia lampra* (Watson, 1879). Apical, apertural, and basal views of holotype of *Basilissa lampra*, BM(NH) 1887.2.9.348, height 7.5 mm, maximum diameter 12.2 mm. **Figures 9, 10.** *Asthelys munda* (Watson, 1879). Apertural and basal views of holotype of *Basilissa munda*, BM(NH) 1887.2.9.350, height 3.0 mm, maximum diameter 3.3 mm.

guenziella. Moreover, if Schepman's (1908: text fig. 1) illustration of the radula of *R. lampra* is accurate, the odd structure of the cusps of the rhachidian and laterals further separates the two genera. However, the two genera undoubtedly are closely related, and, on the evidence of the radula, both are more closely allied to *Seguenzia* Jeffreys, 1876, than to other genera with similar shell shapes, such as *Carenzia* Quinn, 1983. If the similarities of shells hold between *Rotellenzia* and *Seguenziella*, a narrow, U-shaped anterolateral labral sinus probably exists. However, the chipped lip of the holotype of *R. lampra* prevents direct observation of this feature, and the growth lines give no additional indication, a situation also found in *Seguenziella*.

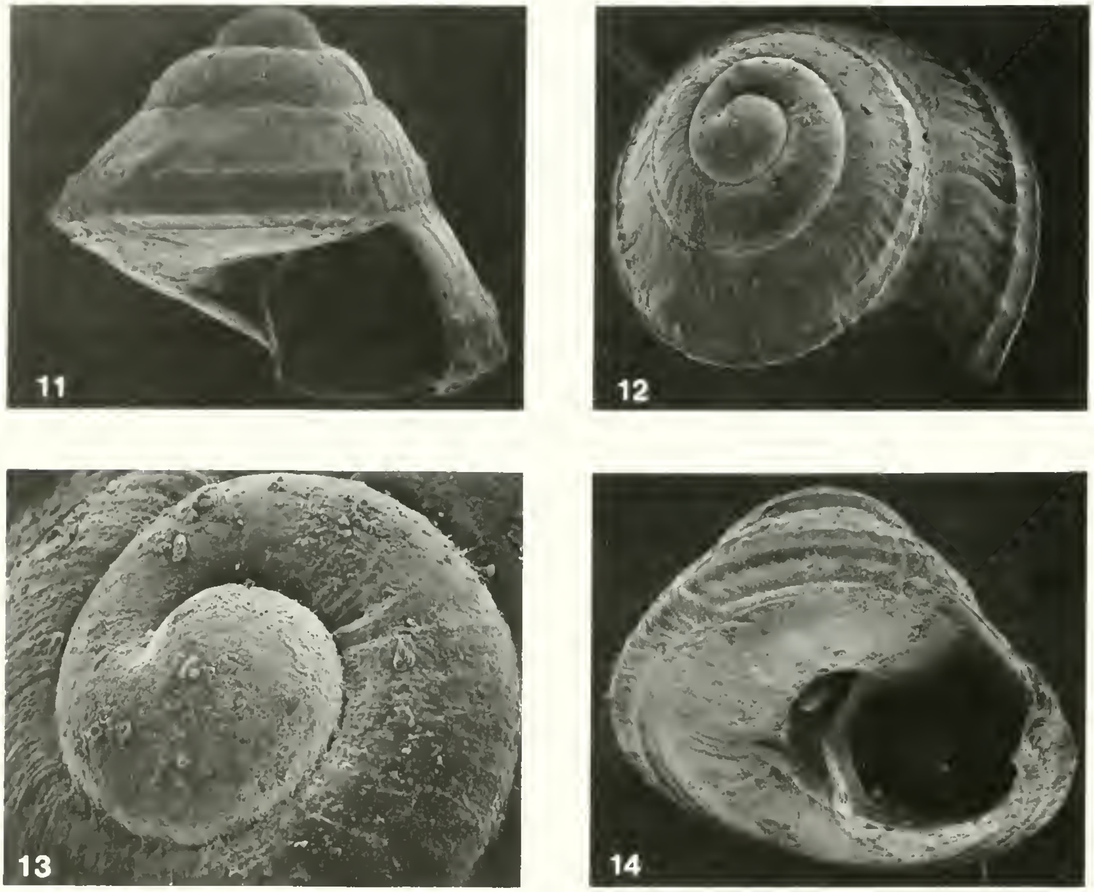
Etymology: From the Latin diminuative of *rota*, a wheel, and *Seguenzia*, a genus of Seguenziidae.

Rotellenzia lampra (Watson, 1879)
(figures 6–8)

Basilissa lampra Watson, 1879:593; 1886:97, pl. 7, fig. 5.—Schepman, 1908:61, text fig. 1.—Cotton, 1959:189.
Seguenzia lampra: Quinn, 1983b:728, fig. 45.

Material examined: 1 specimen, BM(NH) 1887.2.9.348 (holotype); *Challenger* sta. 246, 36°10′N, 178°00′E, 3,749 m; July 2, 1875.

Description: Shell of moderate size (height 7.5 mm, width 12.2 mm), depressed conical, weakly carinate peripherally, umbilicate, thin, iridescent under very thin porcelaneous layer, brass-colored. Protoconch large, about 500 μm in maximum diameter, about 1 whorl. Teleoconch whorls 5.25, spire whorls flat to weakly convex; first 3 whorls with fine, sharp spiral threads, one at midwhorl strongest, subsequent whorls with spirals subequal in strength, all becoming weaker over last 2 whorls; threads number 19 near aperture; last whorl with 2 strong, smooth spiral cords, anterior one peripheral, posterior one close above and along which suture runs, interspace narrow, weakly concave; axial sculpture of low, sharp collabral riblets on first 1.5 whorls, thereafter rapidly disappearing, except near suture where they remain evident as short, comma-like folds. Base weakly convex, umbilicate, with 15 spiral cords (increasing rapidly near aperture to 25), outer 3 rather strong, separated by concave interspaces bearing 3–4 fine spiral threads near aperture, middle 75% of base with 9 broad, flat spiral cords separated by shallow striae, inner 3 cords strong, sharp, separated by concave interspaces with fine, sharp transverse riblets. Umbilicus wide, about 30% maximum shell diameter, funnel-shaped, walls weakly concave, smooth except for growth lines. Aperture trapezoidal; outer lip thin, posterior sinus shallow, broadly V-shaped, apex in posterior 25% of whorl; basal lip thin, basal sinus a wide, very shallow sinuation of lip, apex located in abaxial quarter of base; columella thin, weakly concave in adapical half, weakly convex in abapical half. Operculum unknown. Radula with lanceolate rhachidian, cusp not reflected, finely denticulate along cusp base, unarmed



Figures 11–14. SEM micrographs of *Asthelys munda* (Watson, 1879) from *Porcupine* station 22, USNM 859916. **11.** Apertural view, × 45.5. **12.** Oblique apical view, × 42. **13.** Protoconch, × 126. **14.** Oblique basal view, × 45.5.

distally; lateral with wide, triangular base, long, unreflected cusp on proximal side, finely denticulate along distal edge well back from tip; inner marginal sickle-shaped, edentate.

Measurements: Holotype: height 7.5 mm, width 12.2 mm.

Type-locality: NW of Midway Island, Hawaiian Islands, *Challenger* sta. 246, 36°10′N, 178°00′E, 3,749 m.

Remarks: See under generic remarks.

Asthelys new genus

Seguenzia: Jeffreys, 1877:320 (*partim*).
Basilissa Watson, 1879:593 (*partim*); 1886:96 (*partim*).—Quinn, 1983b:729 (*partim*).

Type-species: *Basilissa munda* Watson, 1879; here designated.

Gender: Feminine.

Diagnosis: Shell small, conical, peripherally bicarinate, umbilicate, nacreous under thin outer porcelaneous layer, white; protoconch large; first 0.5 whorl lacking spiral sculpture, subsequent whorls with strong cord above periphery and strong peripheral cord, together forming weakly bicarinate periphery, weak to strong spiral cords on base, and strong, smooth or pustulate circumumbilical cord; axial sculpture of obscure, sigmoid folds and growth lines; surface microsculpture of microscopic, shallow punctae; base weakly convex; umbilicus narrow, funnel-like; aperture subquadrate; labral sinuses 2, wide, shallow; columella straight or weakly concave. Radula unknown.

Remarks: *Asthelys* most closely resembles *Thelyssina* Marshall, 1983. Shells of both genera are conical with almost flush sutures, lack a midwhorl carina, spiral cord, or angulation on the first teleoconch whorl immediately following the termination of the protoconch, lack strong collabral and spiral microsculpture above the whorl periphery, and have a narrow, funnel-like umbilicus. The type-species of *Asthelys* differs from that of *Thelyssina* by lacking a trochoid tip and terminal rim on the protoconch, having minute punctae instead of vermiculate microsculpture on the first two spire whorls (although *T. sterrha* Marshall, 1983, also has punctations, *fide* Marshall, personal communication), having a bicarinate rather than unicarinate periphery, having a distinct posterior

shell sinus, persistence of the initial spiral cord on all teleoconch whorls, and lacking a strong parietal callus. At least two other species may also be assigned to *Asthelys*: *Basilissa simplex* Watson, 1879, and an undescribed Antarctic species (Marshall, personal communication).

Etymology: Anagram of *Thelyssa*, a genus of Seguenziidae.

Asthelys munda (Watson, 1879)
(figures 9–14)

Seguenzia carinata Jeffreys, 1877:320 (*partim*).
Basilissa munda Watson, 1879:596; 1886:99, pl. 7, fig. 7.—Quinn, 1983b:729. [*Non Basilissa munda* Barsanova, 1966: 150 (misidentification).]

Material examined: 1 specimen, USNM 859916 [(paralectotype of *Carenzia carinata* (Jeffreys, 1877)]; *Porcupine* sta. 22, 56°08′N, 13°34′W, 2,311 m; July, 1870.—1 specimen, BM(NH) 1887.2.9.350 (holotype); *Challenger* sta. 85, 28°42′N, 18°06′W, 2,058 m; August 29, 1873.

Description: Shell very small (height of holotype 3.0 mm, width 3.3 mm), conical, weakly bicarinate peripherally, narrowly umbilicate, thin, iridescent under thin outer porcelaneous layer, white. Protoconch with irregular microsculpture, about 350–375 μm maximum diameter, of about 1 whorl, lacking terminal rim. Teleoconch whorls 4.75; spiral sculpture absent on first half-whorl; fine spiral thread appears on second half-whorl, located at abapical fifth of whorl, gradually strengthening to become subequal to peripheral cord; peripheral cord visible only on last whorl, forming bicarinate periphery with upper spiral cord; axial sculpture present on all whorls, consisting of extremely obscure sigmoid folds, most apparent as undulations of spiral cords; surface microsculpture of microscopic, extremely shallow punctae generally arranged in spiral pattern. Base weakly convex, with 11 spiral cords, innermost strongest, with 8 pustules, and sigmoid transverse rugae and minute punctae. Umbilicus narrow, about 14% of maximum shell diameter, funnel-shaped, walls smooth except for axial growth lines. Aperture subquadrate; outer lip thin, with very wide, shallow, U-shaped posterior sinus, apex located above midwhorl; basal lip thin, with very wide and shallow basal sinus, apex at abaxial third of base; columella almost straight, very weakly concave above, very weakly convex below, slightly thickened, edentate.

Type-locality: W of Palma, Canary Islands, *Challenger* sta. 85, 28°42′N, 18°06′W, 2,058 m.

Remarks: *Asthelys munda* is most similar to *A. simplex* (Watson, 1879), but *A. munda* is smaller, relatively broader, lacks a subsutural spiral cord, and has weaker basal spiral cords, pustulate circumumbilical cord, and less oblique aperture. The specimen from the *Porcupine* Expedition is a juvenile (figures 9–12) from the syntype lot of *Carenzia carinata* (Jeffreys, 1877). The locality of this specimen (NW of Ireland) extends the known range of the species northward more than 2,600 km, indicating a distribution throughout the northeastern Atlantic in depths of about 2,000 m.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold, New York, NY, p. 663.

Barsanova, N. G. 1966. K nachozhdeniyu glubokovodnikh predstavitelei semeistva Seguenziidae (Gastropoda, Prosobranchia) v Tikhom Okeane. [On the finding of deep-sea representatives of the family Seguenziidae (Gastropoda, Prosobranchia) in the Pacific Ocean.] Trudy Instituta Okeanologii 81:144–152.

Bayer, F. M. 1971. New and unusual mollusks collected by R/V JOHN ELLIOTT PILLSBURY and R/V GERDA in the tropical western Atlantic. Bulletin of Marine Science 21(1):111–236.

Boss, K. J. 1982. Seguenziidae. *In:* Parker, S. P. (ed.). Synopsis and classification of living organisms, Vol. 1. McGraw-Hill, New York, NY, p. 973–974.

Clarke, A. H. 1962. Annotated list and bibliography of the abyssal marine molluscs of the world. National Museum of Canada, Bulletin 181:vi + 114 p.

Cossmann, M. 1888. Catalogue illustré des coquilles fossiles de l'Eocène des environs de Paris. III. Annales de la Société Royale Malacologique de Belgique 23:3–324.

Cotton, B. C. 1959. South Australian Mollusca.—Archaeogastropoda. Handbook of the flora and fauna of South Australia. Government Printer, Adelaide, p. 449.

Dall, W. H. 1881. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877–79, by the United States Coast Survey steamer "Blake", Lieutenant-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XV. Preliminary report on the Mollusca. Bulletin of the Museum of Comparative Zoology 9(2):33–144.

Dall, W. H. 1885. List of marine Mollusca comprising the Quaternary fossils and Recent forms from American localities between Cape Hatteras and Cape Roque including the Bermudas. United States Geological Survey, Bulletin 24:1–336.

Dall, W. H. 1889a. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXIX. Report on the Mollusca. Part 2, Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology 18:1–492.

Dall, W. H. 1889b. A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States. Bulletin of the United States National Museum 37:1–221.

Dall, W. H. 1890. Scientific results of explorations by the U.S. Fish Commission steamer "Albatross". VII. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Proceedings of the United States National Museum 12:219–362.

Dall, W. H. 1927. Small shells from dredgings off the southeast coast of the United States by the United States Fisheries steamer "Albatross" in 1885 and 1886. Proceedings of the United States National Museum 70(2667):1–134.

Fischer, P. 1885. Manuel de conchyliologie et de paléontologie conchyliologique, ou historie naturelle de mollusques vivants et fossiles. F. Savy, Paris, p. 689–896.

Goryachev, V. N. 1979. K sisteme glubokovodnikh mollyuskov semeistva Seguenziidae (Gastropoda). [On the system of the deep-sea molluscan family Seguenziidae (Gastropoda).] *In:* Likharev, I. M. (ed.). Molluscs. Main results of their study. Abstracts of communications. Zoological Institute, Akademiya Nauk SSSR, Leningrad, p. 70–71.

Jeffreys, J. G. 1877. New and peculiar Mollusca of the Eulimidae and other families of Gastropoda, as well as of the Pteropoda, procured in the 'Valorous' Expedition. Annals and Magazine of Natural History (4)19:317–339.

Johnson, C. W. 1934. List of marine Mollusca of the Atlantic coast from Labrador to Texas. Proceedings of the Boston Society of Natural History 40(1):1–204.

Keen, A. M. and L. R. Cox. 1960. [Margaritinae]. *In:* Moore, R. C. (ed.). Treatise on invertebrate paleontology. Part I, Mollusca 1. Geological Society of America, University of Kansas Press, Lawrence, KS, p. I249–I251.

Marshall, B. A. 1983. Recent and Tertiary Seguenziidae (Mollusca: Gastropoda) from the New Zealand region. New Zealand Journal of Zoology 10:235–262.

Martens, E. von. 1881. Mollusca. Zoological Record 16:93 p.

Maury, C. J. 1922. Recent Mollusca of the Gulf of Mexico and Pleistocene and Pliocene species from the Gulf states. Part 2: Scaphopoda, Gastropoda, Amphineura, Cephalopoda. Bulletins of American Paleontology 9(38):34–142.

Okutani, T. 1982. Rediscoveries of an abyssal trochid, *Basilissa superba* Watson from the south of Japan. Venus, Japanese Journal of Malacology 40(4):237–239.

Pilsbry, H. A. 1889. Trochidae, Stomatiidae, Pleurotomariidae, Haliotidae. Manual of Conchology. Series 1, Volume 11. Conchological Section, Academy of Natural Sciences, Philadelphia, PA, p. 519.

Quinn, J. F., Jr. 1979. Biological results of the University of Miami Deep-Sea Expeditions. 130. The systematics and zoogeography of the gastropod family Trochidae collected in the Straits of Florida and its approaches. Malacologia 19(1):1–62.

Quinn, J. F., Jr. 1981. A preliminary overview of the Seguenziidae Verrill, 1884. Bulletin of the American Malacological Union for 1980:74 (abstract).

Quinn, J. F., Jr. 1983a. *Carenzia*, a new genus of Seguenziacea (Gastropoda: Prosobranchia) with the descripion of a new species. Proceedings of the Biological Society of Washington 96(3):355–364.

Quinn, J. F., Jr. 1983b. A revision of the Seguenziacea Verrill, 1884 (Gastropoda: Prosobranchia). I. Summary and evaluation of the superfamily. Proceedings of the Biological Society of Washington 96(4):725–757.

Schepman, M. M. 1908. The Prosobranchia of the Siboga Expedition. Part I. Rhipidoglossa and Docoglossa. Siboga Expedition, Monographie 49[1]a:1–107.

Thiele, J. 1929–35. Handbuch der systematischen Weichtierkunde. 2 vols. Gustav Fischer, Jena, p. 1134.

Watson, R. B. 1879. Mollusca of H.M.S. 'Challenger' Expedition. III. Trochidae, viz. the genera *Seguenzia*, *Basilissa*, *Gaza* and *Bembix*. Journal of the Linnean Society of London, Zoology 14:586–605.

Watson, R. B. 1886. Report on the Scaphopoda and Gasteropoda collected by H.M.S. Challenger during the years 1873–76. Report on the Scientific Results of the Voyage of H.M.S. Challenger. 1873–1876, Zoology 15:1–680.

Wenz, W. 1938. Gastropoda. Allgemeine Teil und Prosobranchia. *In:* Schindewolf, O. Handbuch der Paläozoologie, Band 6, Teil 1, Leiferung 1&2:1–480.

Good Hosts and Their Guests: Relations Between Trochid Gastropods and the Epizoic Limpet *Crepidula adunca*

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ABSTRACT

The suspension-feeding calyptraeid limpet-like gastropod *Crepidula adunca* (Sowerby) is found chiefly on the shells of other gastropods in the temperate northeastern Pacific. In the San Juan Islands (Washington, USA), its only host is the trochid *Calliostoma ligatum* (Gould). Experiments in the laboratory showed that *Crepidula* was protected from predation by the sea-star *Leptasterias hexactis* by virtue of its close fit on the host shell and by the effective escape response of *Calliostoma* to sea-stars. The added weight of *Crepidula* (up to 24% of combined weight of guest and host) reduced escape speed and increased the time required for hosts to right themselves after falling in an aperture-up orientation.

INTRODUCTION

Intimate associations between host and guest species are widespread among bottom-dwelling marine organisms. Such associations—parasitisms, commensalisms, and mutualisms—may arise for any of several reasons. In the first place, there are apt to be benefits to the guest. These include a greater and more predictable food supply, greater protection from enemies, and shelter from harsh physical conditions. The suitability of a given species as host depends on its abundance, defenses against potential enemies, and extent to which it is able to provide benefits. If the presence of the guests improves the host's own performance in coping with surroundings, selection in favor of traits facilitating the association would be especially strong.

The present paper is the first in a projected series on the evolution of one widespread but little studied type of intimate association among marine species, that of epizoic limpet-like gastropods living on the shells of other invertebrates. We report here on the association of the temperate northeastern Pacific calyptraeid limpet-like gastropod *Crepidula adunca* (Sowerby) (hereafter known as *Crepidula*) with two trochid gastropod hosts, *Calliostoma ligatum* (Gould) and *Tegula funebralis* (A. Adams) (hereafter known as *Calliostoma* and *Tegula*, respectively). Specifically, we investigated the host distribution of *Crepidula*, the predators of *Calliostoma*, the effect of *Crepidula* on the antipredatory performance of its host in the laboratory, and some factors that render *Calliostoma* an especially suitable host for *Crepidula*.

This research was carried out during May and June, 1986, as part of a field course on functional morphology and evolution given at the Friday Harbor Laboratories (Friday Harbor, Washington, USA) by A. R. Palmer and the senior author, with assistance from R. B. Lowell.

MATERIALS AND METHODS

The distribution of *Crepidula* among hosts was assessed at several localities in Washington and California. Experimental work was conducted with *Calliostoma* and *Crepidula* from Lime Kiln Light (San Juan Island, Washington) and with *Tegula* and *Crepidula* from Tatoosh Island (Washington).

As a first step in the identification of potential predators of *Calliostoma*, a field collection of all available "dead" shells (either empty or occupied by hermit crabs) was made at Lime Kiln Light. Shells were categorized as intact, lethally broken (the apex removed, the lip broken back, or one or more holes of irregular shape through the shell wall), or drilled. Next, *Calliostoma* with epizoic *Crepidula* were maintained in the laboratory with three species of predator that commonly co-occur with *Calliostoma* in the lower intertidal zone. Three crabs (male *Cancer oregonensis* Rathbun, 29.0–44.2 mm in carapace width) were maintained for 9 days with 10 *Calliostoma* each bearing an epizoic *Crepidula*. Another 30 *Callios-*

toma with epizoic *Crepidula* were kept with 15 *Nucella lamellosa* (Gmelin), a drilling muricacean gastropod, for 4 days. The sea-star *Leptasterias hexactis* (Brandt) in preliminary trials was offered *Calliostoma* with epizoic *Crepidula* as well as *Crepidula* that had been removed from their hosts and allowed to attach to the floor of an aquarium before sea-stars were introduced.

All subsequent work involving predation concentrated on how *Calliostoma* protects *Crepidula* from predation by *Leptasterias*. In the first experiment, 20 *Crepidula* ranging in apertural length from 6.5 to 9.5 mm were removed from their original hosts and transplanted onto 10 living *Calliostoma* and 10 empty *Calliostoma*. All *Crepidula*-bearing *Calliostoma* (18.7–21.8 mm in longest dimension) were then glued to square pieces of Plexiglas, 3 cm on each side, with Z-Spar (Koppers Company Inc., Pittsburgh, PA 15219, USA), a quick-setting underwater epoxy-putty, and placed in an aquarium with 30 *Leptaserias* (48–78 mm in diameter) for 7 days. Glue was applied to the shell base in such a way that the aperture was oriented obliquely to the floor of the aquarium, so that the snail's foot was able to attach to the substratum and capable of reaching the shell's apex. Moreover, the foot was free to reach the shell's apex, as would be the case in free-roaming individuals. If differences in the mortality of *Crepidula* did appear between those on living and empty *Calliostoma*, they would be accounted for by traits of the host's soft parts and not by the locomotor performance of the host or the precision of the *Crepidula*'s fit on the host. None of the transplanted *Crepidula* had as close a fit on the new host as they did on their original hosts.

In order to evaluate how the locomotor performance of *Calliostoma* affects *Crepidula*, we ran a laboratory trial for 2 days with 10 glued *Calliostoma* (16.9–20.8 mm long), 10 free-roaming *Calliostoma* (16.2–25.0 mm long), and 18 *Leptasterias*. Each *Calliostoma* bore a *Crepidula* (8.5–12.0 mm long) which was found on it in the field and which therefore conformed precisely to the shell contour of the host.

The presence of *Crepidula* potentially influences the escape of the host from slow-moving predators like sea-stars. In this study, we focused on three factors of importance in the escape of *Calliostoma* and *Tegula* from sea-stars, and on how *Crepidula* affects the host's escape performance in the laboratory. These were (1) the speed of flight, (2) orientation of the host on the aquarium floor after the snail is dropped from a vertical surface (a simulation of what happens when the snail drops from the substratum upon contact with a sea-star), and (3) the time needed to right the shell if the snail fell with aperture (and foot) facing up.

Escape speed of *Calliostoma* and *Tegula* was measured in an aquarium at a temperature of 11.5–13.0 °C. After 2 min of acclimation to the aquarium, each snail was touched for 3 sec with the tube foot of the sea-star *Pycnopodia helianthoides* (Brandt) on the cephalic tentacles. The snail then reared up, rotated 180°, and began its escape. The speed of escape was measured from the time that flight began. Traces of the snail's movements were drawn on a clear plastic sheet that was taped to the underside of the clear Plexiglas aquarium. String was then placed along the trace, cut, and measured according to the path followed by the snail for each interval of 30 sec until the snail encountered the wall of the aquarium. Tests were conducted on snails naturally lacking *Crepidula*, snails with naturally fitted *Crepidula* whose immersed weight in sea-water was less than 10% of the combined weight of host and guest, and snails with naturally fitted *Crepidula* whose immersed weight accounted for 10% or more of the total weight of host and guest.

Orientation of hosts after falling from a vertical surface was assessed for individuals with and without *Crepidula*. Snails held as if they were clinging to a vertical wall of an aquarium were touched with a tube foot and then allowed to fall through 31.5 cm of water to the bottom. Orientation upon landing was considered to be either aperture-up or aperture-down. Three trials were done on each snail.

The time required for snails landing aperture-up to right themselves after a fall was measured for *Calliostoma* and *Tegula* with and without epizoic *Crepidula*. After unsuccessful trials with bottoms of sand, small gravel, and smooth Plexiglas (substrata on which the snails were unable to right themselves), a 6 mm plastic mesh was used as the substratum on which righting was assessed. The holes in the mesh were smaller than the smallest linear dimension of the snail's foot. Righting was divided into two phases: (1) attachment of the foot to the substratum, and (2) placement of the shell over the foot.

RESULTS

Host Specificity of *Crepidula*

At the sites we have investigated, *Crepidula adunca* were found as adults only on the shells of other animals, chiefly gastropods (Table 1). The trochid *Calliostoma ligatum* was the only host at San Juan Island. On the outer Pacific coast of Washington and British Columbia, we have also seen *C. adunca* on *Amphissa columbiana* (Dall), *Searlesia dira* (Reeve), and *Tegula funebralis*. *Tegula* is not found at San Juan Island, but *Amphissa* and *Searlesia* are common there; yet they lacked epizoic *Crepidula*. *Calliostoma*, some with epizoic *Crepidula*, is common on the outer Pacific coast together with the other hosts. In the vicinity of Monterey, California, *C. adunca* is apparently restricted to *Tegula funebralis* (see also Putnam, 1964). Juvenile *C. adunca* are found on adult *Crepidula* as well as on the other hosts mentioned.

Crepidula was the only organism found living on the shells of living *Calliostoma*. By virtue of its ability to extend the foot over the whole shell surface (Harrold, 1982), *Calliostoma* is apparently able to prevent settlement of epizoans other than *Crepidula* (figure 1). Shells of *Calliostoma* occupied by hermit crabs have a variety of epizoans, including small limpets (*Tectura scutum*

Table 1. Occurrence of *Crepidula adunca* on hosts at various sites in the northeastern Pacific.

Locality and host	N	Incidence (%)
San Juan Islands, Washington, May–June, 1986		
Lime Kiln Light		
Calliostoma ligatum (Gould)	179	41
Hermit crabs in *C. ligatum*	74	3
Searlesia dira (Reeve)	36	0
Amphissa columbiana (Dall)	8	0
Margarites pupillus (Gould)	24	0
Nucella lamellosa (Gmelin)	26	0
Peavine Pass, 10 fathoms		
C. ligatum	20	55
A. columbiana	20	0
Rock Point, 40 fathoms		
C. ligatum	31	0
Amphissa spp.	97	0
Trichotropis cancellata (Hinds)	111	0
Margarites spp.	11	0
Hermit crabs	109	0
Central California, March, 1980		
Pacific Grove, intertidal		
Tegula funebralis (A. Adams)	89	26
T. brunnea (Philippi)	50	0
Other gastropods	100	0

Eschscholtz and *Acmaea mitra* Eschscholtz), barnacles, serpulid polychaetes, and the bryozoan *Tubulipora* sp. *Tegula* does not extend its foot up to the shell apex, and apparently cannot prevent settlement of epizoans on the outer shell surface. Of 22 living *T. funebralis* from Tatoosh Island, seven (32%) bore *Crepidula* and nine (41%) bore serpulids, barnacles, or coralline red algae. Three individuals bearing *Crepidula* also had other epizoans growing on the shell. *Crepidula* itself also carried various combinations of corallines, bryozoans, and serpulids.

Predators of *Calliostoma*

An analysis of "dead" shells of *Calliostoma* from Lime Kiln Light suggested that drilling is not a cause of death, and that breakage may be less common than those forms of death that leave the shell intact. Of 78 shells collected, 61 (78%) were intact and 17 (22%) were lethally broken. The proportion of broken shells may have been underestimated owing to the fact that apical fragments may have been lost quickly from the supply of shells available to hermit crabs.

Laboratory trials indicated that the crab *Cancer oregonensis* is a potential predator of both *Calliostoma* and *Crepidula*. Over a 9-day period, three out of 10 *Calliostoma*, as well as three out of 10 *Crepidula* epizoic on the victims, were eaten by the three male crabs. The broken shells of *Calliostoma* closely resembled the damaged "dead" shells collected at Lime Kiln Light.

Figure 1. *Crepidula adunca* epizoic on *Calliostoma ligatum* from Lime Kiln Light, San Juan Island, Washington. Photograph by R.B.L.

None of the 30 *Calliostoma* maintained with 15 *Nucella lamellosa* for 4 days was eaten. This finding corroborated the field evidence that *Calliostoma* was not drilled.

Several sea-stars include *Calliostoma* in their diet and leave the shell intact after the prey is consumed. They include *Pycnopodia helianthoides* (Shivji *et al.*, 1983), *Orthasterias koehleri* (Mauzey *et al.*, 1968), *Stylasterias forreri* (Mauzey *et al.*, 1968), *Pisaster giganteus* (Harrold, 1982), and *Leptasterias hexactis* (Hoffman, 1981). *Calliostoma* has well-developed escape responses to these sea-stars (Hoffman, 1981; Harrold, 1982). We concentrated our work on *Leptasterias*, which attacks its prey by everting the stomach into the aperture and digesting the flesh externally. Not only is *Leptasterias* abundant in the low intertidal habitat of *Calliostoma*, but in preliminary trials this sea-star ate naturally fitted guests as well as their hosts that had been confined with *Leptasterias* in mesh cages under water. We suspected that a good fit of the guest on the host, together with the host's escape reaction, protected *Crepidula* from predation by sea-stars.

Trials with 10 *Crepidula*-bearing free-roaming *Calliostoma* kept with six *Leptasterias* for 7 days resulted in the predation of four hosts and no guests. In another trial, three *Leptasterias* during a 16-hr period ate four of eight *Crepidula* that had been allowed to attach to the floor of an aquarium after being removed from their hosts.

Imprecisely fitted *Crepidula* apparently gained no

Table 2. Escape speeds of *Calliostoma ligatum* in response to contact with the sea-star *Pycnopodia*. Snails that were used either bore naturally fitting *Crepidula* or were found in the field to lack epizoic *Crepidula*.

Category	Trials	Escape speed (cm/sec) with SD
Crepidula lacking	5	0.34 ± 0.037
Crepidula less than 10% of total weight	4	0.32 ± 0.022
Crepidula greater than 10% of total weight	12	0.27 ± 0.070

Table 3. Effect of *Crepidula* on landing orientation of hosts after the latter fall from a vertical surface.

Category	Trials	Percent landing aperture-down
Calliostoma with *Crepidula*	180	23%
Calliostoma from which *Crepidula* were removed	132	10%
Calliostoma naturally without *Crepidula*	39	21%
Tegula with *Crepidula*	21	5%
Tegula from which *Crepidula* were removed	45	18%

protection from sea-stars by their association with living *Calliostoma* if the latter were unable to escape. In the experiment with transplanted *Crepidula* on living and empty *Calliostoma*, mortality of *Crepidula* was the same (five of 10 individuals) whether the host shell was empty or contained a living snail. In addition to preying on *Crepidula*, *Leptasterias* ate seven of 10 living *Calliostoma*.

The effects of a close fit and of the host's escape were further demonstrated by the pattern of attack by sea-stars in the experiment with immobile (glued) and free-roaming *Crepidula*-bearing *Calliostoma*. After the first 9 min of the experiment, nine of 10 free-roaming hosts had already crawled from the floor of the aquarium to just above the surface of the water on the vertical walls of the aquarium. Of the 10 *Calliostoma* attacked by *Leptasterias* during the first 4 hr of the experiment, eight were immobile and only two were free-roaming. This difference was significant at the 0.05 level (two-by-two contingency test). After 2 days, *Leptasterias* had consumed seven of 10 glued *Calliostoma*, three of 10 free-roaming *Calliostoma*, and none of the *Crepidula*.

Escape was not the only defense of *Calliostoma* against *Leptasterias*. Of the 42 cases of subjugation of *Calliostoma* by *Leptasterias* that we witnessed, at least 19 (45%) were unsuccessful. The latter figure is almost certainly an underestimate, because we were unable to monitor the animals continuously. In the 19 unsuccessful attacks, *Leptasterias* was found to be humped over the prey and to have extruded the stomach into the aperture in the usual way, but the sea-stars were unable to push aside the tightly fitting operculum of the retracted gastropod. When the sea-stars released the *Calliostoma*, the latter remained withdrawn for some time before resuming normal crawling activity. The average time required for *Leptasterias* to subdue and consume *Calliostoma* was 2 days.

Effect of the Guest on the Host

Crepidula could have several detrimental effects on its host. In the first place, it adds substantial weight to the animal. *Crepidula* accounted for a mean of 10.2 ± 5.3% of the immersed weight of the host and guest combined (range 1.0–23.8%, $n = 57$). For *Tegula* and *Crepidula*, the mean contribution of *Crepidula*'s immersed weight was 7.3% (range 0.9–16.0%, $n = 7$).

The added weight of *Crepidula* could reduce the locomotor performance of *Calliostoma* during escape attempts from sea-stars. Compared to individuals lacking *Crepidula*, *Calliostoma* with a load of *Crepidula* greater than 10% of total immersed weight moved 20% less rapidly upon being touched by a tube foot of *Pycnopodia* ($p < 0.05$, see Table 2). *Calliostoma* with a moderate load (less than 10% of immersed weight) of *Crepidula* moved at intermediate speeds, but did not differ statistically from the heavily weighted or the *Crepidula*-free snails.

Data in Table 3 on landing orientation indicate that

Table 4. Effect of epizoic *Crepidula* on the time required by hosts to right themselves after landing aperture-up. Differences between *Calliostoma* with and without *Crepidula* were statistically significant at $p < 0.001$ for both the foot-attachment (first) and shell-positioning (second) phases of righting. For *Tegula*, differences for the first phase and for the righting process as a whole were significant at $p < 0.02$.

Category	Trials	Time in seconds with SD: Phase 1	Phase 2
Calliostoma with *Crepidula*	180	82 ± 185	6.2 ± 11
Calliostoma without *Crepidula*	132	34 ± 21	1.2 ± 1.2
Tegula with *Crepidula*	21	774 ± 257	0.24 ± 0.77
Tegula without *Crepidula*	28	527 ± 420	0.84 ± 0.44

epizoic *Crepidula* had an inconsistent effect on its host. The chance of the host's landing aperture-down, enabling the snail to begin crawling away sooner, was greater for *Crepidula*-bearing *Calliostoma* than for individuals whose *Crepidula* were removed, but snails naturally lacking *Crepidula* had the same rather high probability of landing aperture-down as did individuals with epizoic *Crepidula*. *Tegula* with *Crepidula* were less likely to fall aperture-down than were individuals without epizoic *Crepidula*.

The time required for hosts to right themselves after landing in an aperture-up position was significantly greater in individuals bearing *Crepidula* than in those same individuals from which the *Crepidula* had been removed (Table 4). In *Calliostoma*, this was true for both the foot-attachment and the shell-positioning phases of the righting process, whereas in *Tegula* the pattern was due entirely to the first (foot-attachment) phase. The presence of *Crepidula* increased the time of righting by factors of 2.5 and 1.5 in *Calliostoma* and *Tegula*, respectively.

DISCUSSION

Our study of *Crepidula adunca* showed that this species is more or less specialized to live as an epizoan on the shells of living gastropods. Hoagland (1977a) reported that the species has also been collected from the surfaces of subtidal stones, but we have never found *C. adunca* on substrata other than the shells of gastropods and a few hermit crabs despite extensive dredging on all types of bottom in the San Juan Islands. In its apparent restriction to the shells of other animals, *C. adunca* resembles the tropical Eastern Pacific *C. incurva* (Broderip), but the latter species is found on many gastropod hosts as well as on hermit crabs (Vermeij, unpublished data) whereas *C. adunca* is apparently absent from most potential host gastropods with which it lives in the lower intertidal and subtidal zones. The eastern North American *C. convexa* (Say) may live on the shells of gastropods (Hoagland, 1977b), but it is more common on shells occupied by hermit crabs (Karlson & Cariolou, 1982; Shenk & Karlson, 1986), and also frequently adheres to stones and seagrasses (Hoagland, 1977a,b). Among species that have been ecologically characterized, therefore, *C. adunca* ranks as one of the most specialized with respect to the range of substrata occupied.

As sedentary filter-feeders, adult *Crepidula* would in general be highly vulnerable to many kinds of predators, as well as to competitors and physical calamities. Species that characteristically live on exposed surfaces of stones or rocks tend to be large, thick-shelled, and sometimes spiny, whereas most species (except *C. incurva*) living on the outer or inner surfaces of shells tend to be small and thin-shelled. That shells provide a refuge from predators is suggested by our data. Although *C. adunca* that were artificially removed from their host readily fell victim to *Leptasterias*, epizoic individuals were rarely eaten by this predator by virtue of the effective escape responses of *Calliostoma ligatum*, one of its chief hosts. A similar benefit of living on the shells of mobile trochids (*Austrocochlea constricta* Lamarck) was demonstrated by Mapstone *et al.* (1984) in experiments with the grazing epizoic lottiid limpet *Patelloida mufria* (Hedley) in New South Wales, but in this case the chief predator was the muricacean gastropod *Morula marginalba* (Blainville).

Our results may be criticized for having been obtained under controlled laboratory conditions rather than in the field. We believe, however, that the types of field experiment used by Mapstone *et al.* (1984), in which limpets with and without host snails were maintained with and without predators in cages, introduce the same kinds of limitations that are imposed by conditions in the laboratory. Another objection—our lack of replication of some of the experiments—was forced upon us by insufficient time.

We do not know if *Crepidula* gains any substantial protection from its hosts in encounters with other predators. Preliminary trials showed that *Calliostoma* as well as epizoic *Crepidula* were attacked successfully by the crab *Cancer oregonensis*.

Our data indicate clearly that the presence of *Crepidula* decreased the locomotor performance of hosts during escape attempts from sea-stars. To what extent the decrease in escape speed and the increase in the time required for righting the shell after a fall place *Calliostoma* and *Tegula* at greater risk to predation in the field cannot be determined at present. In a similar case, Schmitt *et al.* (1983) showed that when the Californian trochid *Norrisia norrisi* (Sowerby) attempted to escape from *Pisaster giganteus*, its escape velocity was decreased in the presence of the epizoic barnacle *Megabalanus californicus*, and that this decrease resulted in a higher success rate for *Pisaster*.

It is likely that weight rather than drag is responsible for the decrease of the snail's locomotor performance in the presence of epizoic *Crepidula*. At the relatively low velocities of most gastropods, drag is low (Palmer, 1980).

Crepidula may benefit from its association with snails in ways that we did not investigate. The fact that *Calliostoma ligatum* is capable of cleaning its shell and laying down a thin film of mucus on the outer shell surface suggests that settlement of potential competitors such as bryozoans, barnacles, and algae is usually prevented. How juvenile *Crepidula* are able to settle and stay on *Calliostoma* when the latter's foot is extended over the shell is not known. It is also possible that the mucus may contribute to, or help trap, *Crepidula*'s food supply. A possible benefit of *Crepidula* for its hosts is that it increases the effective size of the host, so that potential predators would have greater difficulty in subduing the host. A potential disadvantage of the association to *Crepidula* is that the guest is exposed to desiccation and is prevented from feeding when the host crawls out of water. A similar disadvantage was noted by Mapstone *et al.* (1984) for *Patelloida mufria* on *Austrocochlea constricta*, but in that case the limpet tended to be found chiefly on the underside of the host's shell

where the guest is less at risk to desiccation, whereas in the present instance the guest often occurs on the upper surface of the shell. Adult (female) *Crepidula* are sedentary, and are therefore incapable of moving to the safer underside of the host.

Compared to other species in its size range, *Calliostoma ligatum* is the fastest among the low intertidal gastropods in the San Juan Islands (Miller, 1974). This fact suggests that other potential hosts would pose greater risks for epizoic *Crepidula*. We do not know why *Searlesia* and *Amphissa* serve as hosts on the outer Pacific coast whereas they are not occupied by *Crepidula* in the San Juan Islands. *Searlesia* seems to be avoided by seastars, and it would therefore seem to be a good host for *Crepidula* wherever it occurs; but the animal is very slow, it extends higher into the intertidal zone than does *Calliostoma*, and its shell is extensively grazed by small patellacean limpets.

Although mobility of the host may be an important attribute protecting epizoic *Crepidula* and some other limpets such as *Patelloida mufria*, it may have little to do with the choice of hosts by other epizoic limpets. What these other attributes might be and how they vary geographically are interesting questions for future investigations.

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LITERATURE CITED

Harrold, C. 1982. Escape responses and prey availability in a kelp-forest predator-prey system. American Naturalist 119.132–135.

Hoagland, K. E. 1977a. Systematic review of fossil and Recent *Crepidula* and discussion of evolution of the Calyptraeidae. Malacologia 16:353–420.

Hoagland, K. E. 1977b. A gastropod color polymorphism: one adaptive strategy of phenotypic variation. Biological Bulletin 152:360–372.

Hoffman, D. L. 1981. Defensive responses of marine gastropods (Prosobranchia, Trochidae) to certain predatory sea stars and the dire whelk, *Searlesia dira* (Reeve). Pacific Science 34:231–243.

Karlson, R. H. and M. A. Cariolou. 1982. Hermit crab shell colonization by *Crepidula convexa* Say. Journal of Experimental Marine Biology and Ecology 65:1–10.

Mapstone, B. D., A. J. Underwood, and R. G. Creese. 1984. Experimental analyses of the commensal relation between intertidal gastropods *Patelloida mufria* and the trochid *Austrocochlea constricta*. Marine Ecology Progress Series 17:85–100.

Mauzey, K. P., C. Birkeland, and P. K. Dayton. 1968. Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49:603–619.

Miller, S. L. 1974. Adaptive design of locomotion and foot form in prosobranch gastropods. Journal of Experimental Marine Biology and Ecology 14:99–156.

Palmer, A. R. 1980. Locomotion rates and shell form in the Gastropoda: a re-evaluation. Malacologia 19:289–296.

Putnam, D. A. 1964. The dispersal of young of the commensal gastropod *Crepidula adunca* from its host, *Tegula funebralis*. The Veliger 6(Suppl.):63–66.

Schmitt, R. J., C. W. Osenberg, and M. G. Bercovitch. 1983. Mechanisms and consequences of shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby) (Trochidae): indirect effects of *Octopus* drilling. Journal of Experimental Marine Biology and Ecology 69:267–281.

Shenk, M. A. and R. H. Karlson. 1986. Colonization of a shell resource by calyptraeid gastropods: tests of habitat selection and preemption models. Journal of Experimental Marine Biology and Ecology 99:79–89.

Shivji, M., D. Parker, B. Hartwick, M. J. Smith, and N. A. Sloan. 1983. Feeding and distribution study of the sunflower sea star *Pycnopodia helianthoides* (Brandt, 1835). Pacific Science 37:133–140.

Distribution, Abundance, and Movement Patterns of Shoreline Chitons of the Caribbean Coast of Mexico

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ABSTRACT

Observations of relative numbers, wet weight, distribution, and movements of *Chiton squamosus* and *Acanthopleura granulata* were made during 1983 and 1984 along unsubmerged, wave-washed portions of the rocky shorelines of Akumal and Tulum, Quintana Roo, México. Incidental, less detailed data are presented for *Chiton marmoratus*, *Ceratozona squalida*, and *Chiton tuberculatus*. *Chiton squamosus* was most abundant at Tulum in exposed, wave-washed situations well above mean sea level; *A. granulata* occurred in lower, more protected areas, and was most common in shore-margin pools at Akumal. *Chiton marmoratus* was less common than the former two species, and usually occurred in areas exposed to wave action in three morphotypes. *Ceratozona squalida* and *C. tuberculatus* were uncommon above mean low water level. Numerical densities of *C. squamosus* ranged from 0.3/m^2 to 13.9/m^2, depending upon habitat type; biomass densities ranged from 0.3 g/m^2 to 28.2 g/m^2. Numerical density of *A. granulata* ranged from 0.1/m^2 to 16.4/m^2, biomass density from 0 g/m^2 to 54.9 g/m^2. July and December size distributions and total numbers are presented for *C. squamosus* and *A. granulata* at four subsites of each major research area. Numbers of *C. squamosus* at three Tulum subsites were reduced following severe summer storms. Movements of both *C. squamosus* and *A. granulata* were primarily nocturnal, although some individuals of each were active diurnally. Nocturnal movement by individual chitons usually was discontinuous. Comparison of total distances moved with total displacements from original sites suggested tendencies to travel within restricted areas.

INTRODUCTION

Although the marine invertebrates of the Caribbean Sea have been studied with considerable intensity, reports dealing with the invertebrate fauna from the northwestern shores of these waters are relatively scarce. Research on chitons reflects this situation well; although a number of works on various aspects of the biology of West Indian species exist (see Glynn, 1970, for references), the species of the western shores of this sea have been relatively neglected and typically are represented casually in publications dealing with general molluscan faunas (*e.g.*, Weisbord, 1926; Jaumé, 1946; Hidalgo, 1956; Vokes, 1983). Here, we list the chitons of the rocky shoreline of a restricted segment of the eastern coast of the Yucatán Peninsula and discuss in preliminary fashion various aspects of the ecology of *Chiton squamosus* and *Acanthopleura granulata*, the two most common chitons there.

STUDY AREA AND METHODS

Our study sites are at Akumal (20°24′N, 87°18′W) and Tulum (20°13′N, 87°26′W), Quintana Roo, México. In this area, sandy embayments alternate with rocky headlands of dark limestone, eroded remnants of Pleistocene reefs. Fringing, live reefs lie from several hundred to nearly a thousand meters offshore. During much of the year, the easterly tradewind sweeps the coast; variations in water level at the shoreline appear to be more a function of wind velocity and direction than that of the minor semidiurnal tidal changes (less than 0.3 m; data from tide tables for Key West, Florida, USA corrected for Belize City, Belize, 325 km S Akumal) that occur along this coast.

At Akumal, a shallow (maximum depth 1.5–4 m), crescentic bay approximately 1 km broad and 500 m deep is protected at its seaward boundary by a living coral reef. The flanking, northern margin of the bay is a flat, weathered Pleistocene reef-limestone headland, fragmented at its seaward fringe, and rising shallowly from sea level at its outer edge to only several meters above sea level at its junction with the forebeach. In 1983, six pools (subsites) were selected from along the seaward margin of this headland for surveys of numbers and densities, and for observations of movements of chitons; only data from four of these are presented here. All were within 10 m of the sea margin and were filled and drained by wave action for at least part of each day. In some areas of these pools, chitons were exposed to conditions of drying and direct sunlight. Crude measurements along the longest axis of each pool and along the longest axis perpendicular to this were taken; in addition, two pools

were measured more accurately and were drawn to scale on graph paper to allow calculations of chiton densities. Pool 1 measured 7.0 × 4.6 m; Pool 3, 11.6 × 1.8 m; Pool 5, 7.3 × 4.6 m; Pool 6, 4.3 × 2.7 m. Water depth within pools usually ranged from less than 0.3 m to approximately 0.8 m. During the storms of July 2–18, 1983, pools frequently were totally immersed by the sea for several hours to longer than one day. Various pools were surveyed for size class, numbers, and species of chiton on July 20 and December 15, 1983; other, less detailed surveys were made prior and subsequent to these dates.

At the Tulum site, the coast is sublinear; steep limestone cliffs (remnants of the Pleistocene reef) rise directly from the sandy bottom, or from a litter of very large to small breakdown boulders. A fringing reef lies approximately 0.5 km offshore. Horizontally, much of the cliff base and breakdown is below water for most of the day and wave splash usually precludes drying. A zone of multicellular reddish- to greenish-brown adherent algal vegetation coats the lowest portions of most cliff faces and breakdown rubble from the sandy bottom extending upward from several cm to 1.2 m. On this (windward) coast, the vertical limit of this vegetation probably is the product of a number of physical (wind direction and intensity, mean and extreme low tide, *etc.*), and possibly, also, biotic factors (Duggins and Dethier, 1985).

At Tulum, the plane of the upper level of this algal zone served as our major vertical reference point. Lacking calm conditions during the study, we could not determine tidal stands here with accuracy, but feel that the zone's upper level more nearly approximates mean high, rather than mean low, water level. Chitons were far more numerous above (up to 1.8 m above the sandy substrate) than within this vegetation, and only those above and a few easily visible within the upper 30 cm of the zone were counted in our surveys. Constantly submerged areas were not examined for presence of chitons during this study.

Seven subsites were selected along cliff bases and breakdown rubble; only data for four of these are presented here. Subsite 1 was a moderate-sized, deeply pitted boulder of irregular shape, separated by 1 m from an adjoining rock. Its base was completely submerged to a depth of 0.3–0.6 m at most times; its top usually extended 0.6–0.9 m above sea level, and its circumference at the upper macro-algal limit was approximately 12.2 m. Approximately 75% of its exposed (all but its uppermost) surface was inhabited by chitons. Subsite 2 was an undercut cliff face just N of Subsite 1; approximately 14.3 m of its length was surveyed for chitons. Subsite 5 was a very large, slab-sided boulder separated from other rock surfaces by at least 3 m of sand; most (all but the farthest backside) of its lower circumference was inhabited by chitons; this 28.7 m was surveyed. Subsite 7 was an isolated rock just S of Subsite 5 and surrounded by sand; 12.2 m of its circumference were surveyed. Subsites 1–7 were surveyed on July 20 and 21 and December 13, 1983.

Prior to survey and movement studies, six size classes of chitons were erected as follows: Class 1, those less than 1.27 cm from anterior to posterior tips of girdle; Class 2, those from 1.27 to 2.53 cm; Class 3, 2.54–3.80 cm; Class 4, 3.81–5.07 cm; Class 5, 5.08–6.34 cm; Class 6, 6.35–7.61 cm. To crudely assess biomass, wet weights were taken for five specimens of each species from each of the three size classes which held the greatest number of individuals of that species. Chitons were removed from substrate, blotted dry with a soft cloth, and weighed to the nearest 0.1 g with a Pesola spring balance. After weighing, shell plates were removed from an additional sample of eight formalin-preserved chitons, and weighings were repeated to determine ratios of wet soft part weight to total weight. These ratios were utilized in final calculations of biomass densities.

To investigate movement patterns, individuals of each species were marked with small spots of quick-drying paint and their locations were noted. One to several return visits were made to determine if movement had occurred from the original location of each. At Tulum on June 28, six *C. squamosus* clinging in relatively vertical wave-splashed areas were marked during the period 0545–0750 hr; all were checked near 1700 hr and one was checked twice additionally at 0700 hr on June 28 and at 0600 hr on June 29. At Akumal on July 18, 1983, nine *A. granulata* were marked near 1000 hr and were checked for displacement from original sites twice subsequently on that date; three additional individuals were marked at 0215 hr and checked near 1700 hr. A full dark to daylight vigil was maintained during the night of July 28–29, 1983 (Akumal Pool 2, 2015–0545 hr) to monitor nocturnal movements of both species; a less thorough vigil was undertaken during the night of July 1–2, 1984 at Akumal Pool 3 to gain additional data. On both nights, movements were checked at 15-min intervals.

Voucher specimens of the five species of chiton encountered are deposited in the Recent Invertebrate Collection of the Texas Memorial Museum–The University of Texas at Austin: *C. squamosus*, 1574TX1; *A. granulata*, 1574TX2; *Chiton marmoratus*, 1574TX3, 1574TX4, 1574TX5; *Ceratozona squalida*, 1574TX6; *Chiton tuberculatus*, 1574TX7.

RESULTS

Distribution: *Chiton squamosus* is most numerous in areas exposed to wave action; at Tulum, most adhere to vertical surfaces above the level of the multicellular algae and are kept moist by wave splash or inundation. Here, *Acanthopleura granulata* occurs in lower, more sheltered or concealed locations, among the crevices of cliff breakdown rubble, closer to, and sometimes within the algal zone. *Chiton marmoratus* occurs in three color morphs (Abbott, 1974) and at lower frequency at Tulum than *C. squamosus* and *A. granulata*, but still is relatively common; it represents less than 20% of the entire chiton population here. The reddish morph of *C. marmoratus* is far less common here than the light and dark morphs. The distribution of this species is similar to that of *C.*

Table 1. Numbers of *Chiton squamosus* and *Acanthopleura granulata* at four Tulum subsites on July 20 and December 13, 1983 [1]

Species	Size class	Subsite 1 Jul	Subsite 1 Dec.	Subsite 2 Jul.	Subsite 2 Dec.	Subsite 5 Jul.	Subsite 5 Dec.	Subsite 7 Jul.	Subsite 7 Dec.
C. squamosus	1	1	0	0	—	4	—	0	1
	2	8	0	12	—	32	—	22	18
	3	20	17	36	—	68	—	42	86
	4	25	38	52	—	57	—	35	68
	5	0	3	0	—	0	—	4	3
	6	0	0	0	—	0	—	0	0
	Total	54	58	100	—	161	—	103	176
A. granulata	1	3	0	0	—	0	—	0	0
	2	7	0	0	—	2	—	2	0
	3	6	0	5	—	2	—	0	0
	4	4	7	11	—	3	—	0	0
	5	6	6	4	—	0	—	0	0
	6	0	1	1	—	0	—	0	0
	Total	26	14	21	—	7	—	2	0

[1] December surveys not performed at Subsites 2 and 5.

squamosus, but somewhat closer to the top of the algal zone. *Ceratozona squalida* occurs within, and occasionally above, the zone of algae and forms less than 1% of the non-submerged population visible at this site. *Chiton tuberculatus* is rare; only two were encountered during our surveys.

On the relatively exposed vertical rock faces and rubble at Tulum, *C. squamosus* was more common than *A. granulata* (table 1), although the cryptic distribution of *A. granulata* here results in some degree of underestimation of its abundance. In the shelf-margin pools at Akumal, *A. granulata* was far more common than *C. squamosus* (table 2). No additional species of chiton were observed here. Just beyond the seaward entries and spillways of these pools, in alternately exposed and inundated, heavily surf-swept areas not surveyed, *C. squamosus* were more numerous, and *A. granulata* decreased in frequency.

Biomass: Mean wet weights per most common size classes ($\bar{x} \pm$ SE) of *C. squamosus* were: Class 2, 0.68 ± 0.08 g; Class 3, 1.98 ± 0.23 g; Class 4, 6.28 ± 0.21 g. Those for *A. granulata* were: Class 3, 4.06 ± 0.35 g; Class 4, 8.94 ± 0.29 g; Class 5, 11.40 ± 0.92 g. Ratios of wet soft part weight to total weight were: *C. squamosus*, 0.50; *A. granulata*, 0.43.

Density: Numerical density data for both species were calculated (table 3) and reflect those presented previously for numbers (tables 1, 2) at both sites. Inter-subsite differences in numerical density (table 3) are more pro-

Table 2. Numbers of *Chiton squamosus* and *Acanthopleura granulata* at four Akumal subsites on July 20 and December 15, 1983.[1]

Species	Size class	Subsite 1 Jul.	Subsite 1 Dec.	Subsite 3 Jul.	Subsite 3 Dec.	Subsite 5 Jul.	Subsite 5 Dec.	Subsite 6 Jul.	Subsite 6 Dec.
C. squamosus	1	0	0	0	—	0	—	0	0
	2	0	1	0	—	1	—	1	7
	3	4	12	8	—	15	—	6	8
	4	0	5	1	—	7	—	2	1
	5	0	0	0	—	0	—	0	0
	6	0	0	0	—	0	—	0	0
	Tot.	4	18	9	—	23	—	9	16
A. granulata	1	0	1	0	—	0	—	0	0
	2	3	2	1	—	1	—	4	9
	3	36	24	82	—	9	—	39	78
	4	148	124	269	—	120	—	135	117
	5	16	5	1	—	15	—	5	2
	6	4	0	0	—	0	—	0	0
	Tot.	207	156	353	—	145	—	183	206

[1] December surveys not performed at Subsites 3 and 5.

Table 3. Numerical density (individuals/m²) and biomass density[1] (g m²; in parentheses) for *Chiton squamosus* and *Acanthopleura granulata* at Tulum and Akumal subsites on July 20 and December 13 or 15, 1983.

Site	Subsite	July 20 *C. squamosus*	July 20 *A. granulata*	December 13 or 15[2] *C. squamosus*	December 13 or 15[2] *A. granulata*
Tulum	1	7.5 (14.0)	3.8 (7.7)	8.1 (18.9)	1.9 (7.8)
	2	13.9 (28.2)	2.9 (9.8)	— —	— —
	5	4.3 (6.8)	0.2 (0.4)	— —	— —
	7	7.6 (11.7)	0.1 (—)	12.9 (22.4)	0 (0)
Akumal	1	0.3 (0.3)	15.6 (53.4)	1.4 (2.1)	11.7 (40.8)
	3	0.4 (0.5)	16.4 (54.9)	— —	— —

[1] Biomass densities are based only on size classes 2, 3, and 4 for *C. squamosus* and 3, 4, and 5 for *A. granulata*, hence are conservative (see tables 1 and 2 to assess unincluded specimens).
[2] Tulum surveyed December 13; Akumal, December 15.

nounced at Tulum than at Akumal due to the greater amount of habitat diversity (degree of exposure versus shelter) here; biomass densities in g/m² also reflect this relationship (table 3).

Size distribution: At both Tulum and Akumal, individuals of size Class 4 usually were the most common *A. granulata* during July and December surveys (tables 1, 2). At Akumal, individuals of Class 3 were the most common *C. squamosus* in both surveys (table 2); at Tulum, *C. squamosus* of Class 3 were most common during three surveys, while those of Class 4 were most common in three other surveys (table 1).

Storm effects: A number of storms with severe easterly winds struck our sites during the period of July 2–18, 1983; that on July 16 was particularly severe. Percentage losses of *C. squamosus* at three Tulum subsites between July 7, the date of preliminary surveys at several subsites, and July 20, 1983 (table 1), the date of our main survey, were: Subsite 2, 32%; Subsite 5, 27%; Subsite 7, 29%. By December 13, 1983, the population of *C. squamosus* at Subsite 7, one of two subsites at Tulum surveyed then (table 1), exceeded that of the July 20 survey by 71% and that of the July 7 preliminary survey by 20%. Populations of *A. granulata* at these sites were too small to use in loss estimates (table 1).

Movements: Diurnal displacements of *C. squamosus* marked on June 29 were as follows: Chiton 1) 0715–1700 hr, 35.6 cm; 2) 0715–1700 hr, 0 cm; 3) 0750–1705 hr, 10.2 cm; 4) 0750–1705 hr, 5.1 cm; 5) 0750–1715 hr, 11.4 cm; 6) 0545–0700 hr, 48.3 cm; 0700–1705 hr, 91.4 cm; 1705–0600 hr, 170 cm. Diurnal displacements of *A. granulata* marked on July 18 were as follows: 1) 1000–1350 hr, 7.6 cm; 1350–1710 hr, 0 cm; 2) 1000–1350 hr, 2.5 cm; 1350–1710 hr, 99.1 cm; 3) 1000–1350 hr, 0 cm; 1350–1710 hr, 0 cm; 4, 5, 6) 1015–1430 hr, 0 cm; 1430–1725 hr, 0 cm (all three individuals); 7) 1415–1710 hr, 7.62 cm; 8, 9) 1415–1710 hr, 0 cm. General observations of *C. squamosus* at Tulum and of *A. granulata* at Akumal during census periods also indicated that individuals of the former species were more likely to be in motion during daylight than those of the latter.

Distributive statistics for total time observed, total distance moved, and rate of travel are presented by species and size class for the 1983 nocturnal movement survey in table 4. Individuals of both species moved discontinuously; some remained motionless for more than an hour between bouts of movement; none were active continuously through the night (table 4). Sample sizes were small and did not permit confident comparisons between species or size classes. Displacement of individual chitons from place of initial observation to place of final observation usually was considerably less than 30% of total distance traveled; this suggested either a lack of strongly directional movement or a weak tendency to remain within a home "range". In 1984, distances travelled and rates of travel for 6 *C. squamosus* were approximately 50% those of 1983; those for *A. granulata* were less than 33% of those in 1983.

Table 4. Distributive statistics for nocturnal movements of *Chiton squamosus* and *Acanthopleura granulata* at Akumal Subsite 2 on July 28–29, 1983, during 2015–0545 hr.

Species	Size class	N	Time in motion (hr)[1] $\bar{x}$	Time in motion (hr)[1] SE	Distance moved (cm) $\bar{x}$	Distance moved (cm) SE	Rate (cm/hr) $\bar{x}$	Rate (cm/hr) SE
C. squamosus	3	4	6.68	0.66	106.04	30.89	16.92	5.65
	4	5	7.25	0.41	108.97	18.27	15.14	2.33
A. granulata	2	2	7.13	0.37	194.31	24.13	27.53	4.84
	4	2	8.00	1.25	124.46	68.59	17.32	11.28
	5	2	7.00	2.50	262.89	141.00	34.80	7.71

[1] A 15 min period in which motion occurred was scored as full 15 min of motion; thus time in motion is an overestimation of actual activity.

DISCUSSION

Few works of direct ecological bearing exist for comparison with this study (Glynn, 1970; Kangas & Shepherd, 1984; Duggins & Dethier, 1985; Otaiza & Santelices, 1985). Glynn (1970) found *A. granulata* to be the chiton that occurred highest on the shore in Puerto Rico as did Lewis (1960) at Barbados; these authors did not discuss *C. squamosus*. At Tulum, when the shoreline structure permitted comparisons, *A. granulata* occupied a physical niche similar to those reported by Lewis (1960) and by Glynn (1970), but overlapped approximately the lower 0.3 m of the habitat of *C. squamosus*, which occurred considerably higher and was considerably more numerous at the study site here (table 1). At Akumal, the study site was not comparable physically with those at Puerto Rico, Barbados or Tulum, but *A. granulata* occurred in greater numbers than *C. squamosus* (table 2) in situations that were more protected from wave action. Here, but not at Tulum, *A. granulata* occurred in numerical densities (table 3) approaching those reported by Glynn (1970), suggesting that the presence of *C. squamosus* may serve to limit the numbers or modify (toward crypticity) the distribution of *A. granulata* on Tulum's vertically disposed shorelines. At our sites (table 3), neither chiton reached densities of the four most common intertidal chitons studied in Chile by Otaiza and Santelices (1985), but the average sizes of each of those four species were considerably smaller than those of each of ours (tables 1, 2). The range of densities of a variety of *subtidal* Australian chitons examined by Kangas and Shepherd (1984), with a single exception, fell within that of densities of *C. squamosus* and *A. granulata* at our study sites (table 3). *Chiton marmoratus* was considerably more numerous at the Tulum site than at Glynn's Puerto Rican study area (1970) and, on the unsubmerged portions of the shoreline at Tulum, occurred higher than *A. granulata*, rather than lower, as at Barbados (Lewis, 1960). Both Chilean (Otaiza & Santelices, 1985) and Australian (Kangas & Shepherd, 1984) chitons also displayed the species-specific vertical habitat stratification characteristic of Caribbean sites.

Following hurricanes that struck Turrumote Reef, Puerto Rico, in 1963 and 1967, Glynn (1970) noted 46% and 41% diminutions in numbers of *C. tuberculatus* and *A. granulata*, respectively, in 1968—reductions similar to those observed in *C. squamosus* at Tulum following severe summer storms. Size distributions (table 1) do not elucidate the process of population recovery at Tulum Subsite 7, but suggest migration of adults from other areas less than 3 m distant.

As reported previously by Glynn (1970) for *A. granulata* and *C. tuberculatus* in the eastern Caribbean, *A. granulata* and *C. squamosus* from our study area, fed (indexed by movement) primarily nocturnally, and displayed only weak homing abilities.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold, New York, 663 p.

Duggins, D. O and M. N. Dethier. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. Oecologia 67:183-191.

Glynn, P. W. 1970. On the ecology of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton tuberculatus* Linné: density, mortality, feeding, reproduction, and growth. Smithsonian Contributions to Zoology 66:1–21.

Hidalgo, E. 1956. Algunos moluscos de la Isla de Cozumel, Quintana Roo, Mexico. Acta Zoologica Mexicana 1:1–16.

Jaumé, M. L. 1946. Moluscos marinos litorales del Cabo Catoche, Yucatán, Mexico. Revista de la Sociedad Malacologica "Carlos de la Torre" 4:95–110.

Kangas, M and S. A. Shepherd. 1984. Distribution and feeding of chitons in a boulder habitat of West Island, South Australia. Journal of the Malacological Society of Australia 6:101–111.

Lewis, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. Canadian Journal of Zoology 38:391–435.

Otaiza, R. D. and B. Santelices. 1985. Vertical distribution of chitons (Mollusca: Polyplacophora) in the Rocky Intertidal Zone of central Chile. Journal of Experimental Marine Biology and Evolution 86:229–240.

Vokes, H. G 1983 Distribution of shallow-water marine Mollusca, Yucatán Peninsula, Mexico. National Geographic Society Research Reports 15:715–723.

Weisbord, N. E. 1926. Notes on marine mollusks from the Yucatán Peninsula, Mexico. The Nautilus 39(3):81–87.

Transfer of *Cerithiopsis crystallina* Dall to the Genus *Varicopeza* Gründel, Family Cerithiidae (Prosobranchia: Gastropoda)

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ABSTRACT

The small cerithiid, formerly known as *Cerithiopsis crystallina* Dall, is transferred from the family Cerithiopsidae to the family Cerithiidae, genus *Varicopeza*, on the basis of conchological, radular, and anatomical characters. *Varicopeza crystallina* is the first Atlantic species of a previously monotypic, Indo-Pacific genus. It has an extensive, offshore, geographic distribution throughout the Antilles, Florida, and the Gulf of Mexico.

Key words: Prosobranchia; Cerithiidae; *Cerithiopsis*; *Varicopeza*; systematics; Caribbean.

INTRODUCTION

Examination of numerous lots of a small enigmatic cerithiid-like prosobranch, given the specific name *crystallina* and assigned by Dall (1881:89) with a query to the genus *Cerithiopsis* Forbes and Hanley, 1851, has prompted this paper. "*Cerithiopsis*" *crystallina* Dall, 1881 has been dredged in numerous localities throughout the Antilles, off Florida, and in the Gulf of Mexico. Although common in some museum collections, it is not a well-known species and rarely listed in popular shell books. Dall (1881:89), although initially uncertain of the generic assignment of this species, later (1889:254) allocated it to *Cerithiopsis* with more certitude, and his allocation has been followed by subsequent authors. Despite Dall's (1881:90) final referral of this species to *Cerithiopsis*, he appears to have been uncomfortable with this assignment, as he compared *C. crystallina* with other small dredged cerithiids assigned by Watson (1885) to *Bittium* Gray, 1847. Dall apparently examined some live-collected material, because he described alcohol-preserved animals as having well developed eyes and long tentacles, and a short rounded foot with a circular operculum. He noted that "the opercular lobe appears to have several short processes on each side". To my knowledge, no other published information about this species exists.

A study of conchological features of "*Cerithiopsis*" *crystallina* indicates that this species does not fit the criteria defining *Cerithiopsis* species. Moreover, recent examination of preserved animals and a study of the radula with scanning electron microscopy have provided substantial evidence that *C. crystallina* should not be considered a member of the Cerithiopsidae. The following account presents this evidence and provides a new description and generic assignment.

MATERIALS AND METHODS

Preserved specimens from Spanish Wells, Eleuthera, obtained from the gut of the starfish *Astropecten*, were dissected under a binocular dissecting microscope to study the operculum, radula, and anatomy. Scanning electron micrographs (SEM) were made of the radula, operculum, and shell on a Zeiss-Novascan-30 instrument.

The following abbreviations appear in the text: IRCZM, Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Ft. Pierce, Florida; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; MNHNP, Muséum National

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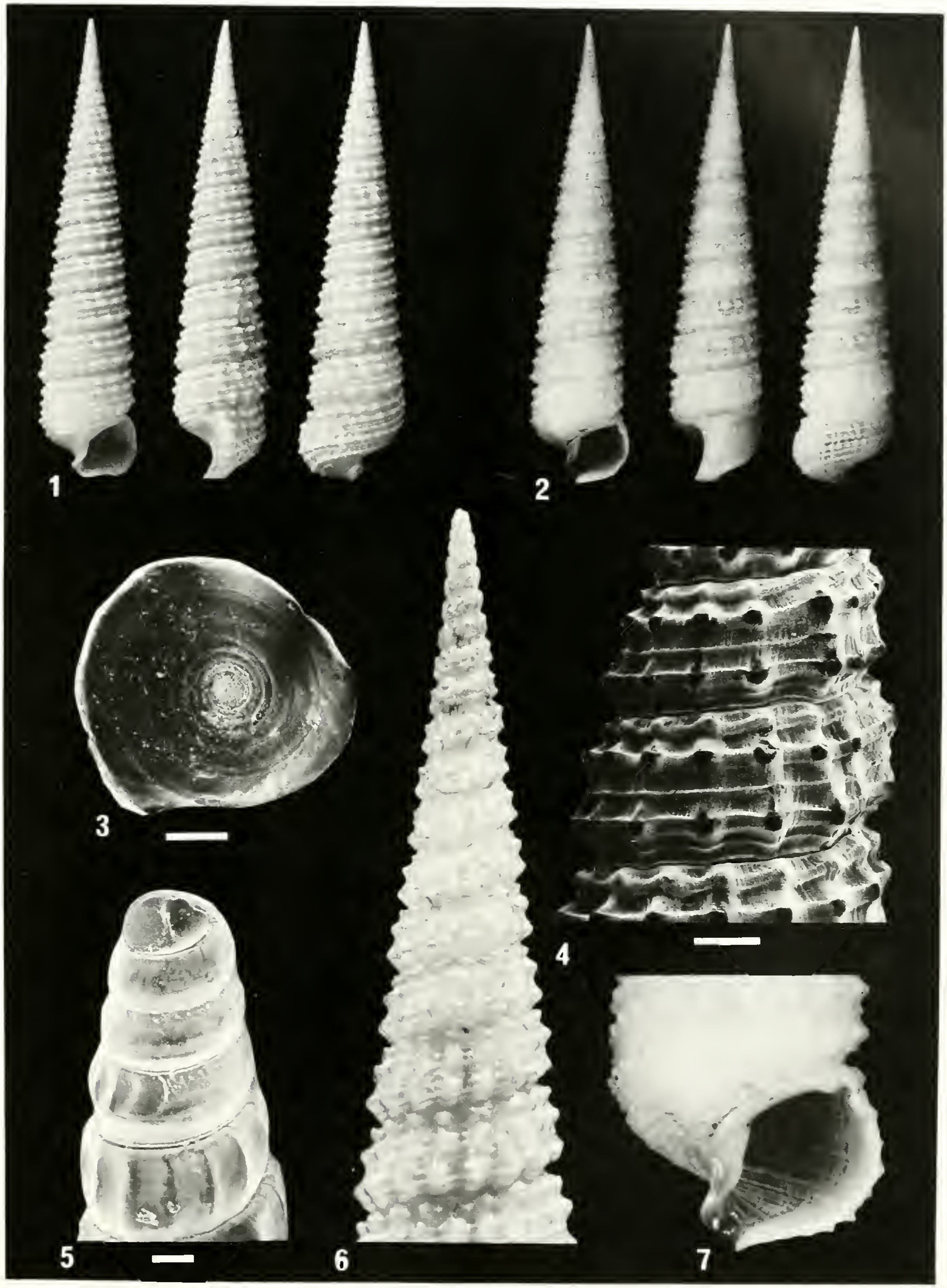
Figures 1–7. *Varicopeza crystallina* (Dall). **1.** Dead collected specimen from 116 fm, off St. Lucia (USNM 810888), 14.41 mm. **2.** Live-collected specimen from 85 fm, Gulf of Mexico, between Mississippi delta and Cedar Keys, Florida (USNM 93763), 17.5 mm. **3.** Scanning electron micrograph (SEM) of operculum from specimen off Spanish Wells, Eleuthera, Bahamas (IRCZM 065: 02228), bar = 200 µm. **4.** SEM detail of midwhorl sculpture on specimen from Spanish Wells, Eleuthera, Bahamas (IRCZM 065: 02228), bar = 300 µm. **5.** SEM of protoconch and early whorls of specimen from 100 fm off Barbados (USNM 87295), bar = 80 µm. **6.** Closeup of early and midwhorls showing sculptural details on specimen depicted in figure 2 (USNM 93763). **7.** Detail of body whorl and aperture from specimen depicted in figure 2 (USNM 93763).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d'Histoire Naturelle, Paris; USBF, United States Bureau of Fisheries; USNM, United States National Museum, National Museum of Natural History, Smithsonian Institution, Washington, DC.

Records and specimens examined: LESSER ANTILLES, Barbados: MCZ 7406, 133 m, RV *Blake*, Sta. 290; MCZ 7394, 182 m, RV *Hassler*, Sta. 1; MCZ 238240, 229 m, West Coast, Barbados; USNM 434158, 434164, 419146, 419147, 419149, 419150, 434167, 434153, 434154, 419148, 430161, 434168, 434159, 434160, 434163, 430162, 810910, 810917, all 150–182 m, RV *Blake*, Sta. 300; Guadeloupe: USNM 434155, 1,605 m, RV *Blake*, Sta. 14; St. Lucia: MCZ 7405, 212 m, RV *Blake*, Sta. 220; USNM 810888, 212 m, RV *Blake*, Sta. 270, 13°50′15″N, 61°03′45″W; Martinique: MCZ 7404, 715 m, RV *Blake*, Sta. 210; Dominica: MCZ 7402, 583 m, Sta. 176; MCZ 7403, 252 m, Sta. 36; St. Croix: MCZ 7399, 7400, 7401, 210–453 m, RV *Blake*, Sta. 128, 132, 134, all off St. Croix. GREATER ANTILLES, Cuba: MCZ 7395, 1,472 m, RV *Blake*, Sta. 2, off Morro Light, Havana (holotype); MCZ 7398, 823 m, RV *Blake*, Sta. 51, off Havana; MCZ (no number), 344 m, RV *Blake*, Sta. 5, off Santiago; MCZ (no number), 457 m, RV *Atlantis*, Sta. 3490, off Havana (23°11′N, 81°55′W); USNM 93832, 369 m, RV *Blake*, Sta. 2131, S of Cuba; USNM 94109, 366 m, RV *Blake*, Sta. 2135, S of Cuba; Puerto Rico: USNM 161327, Aqadilla. BAHAMAS: USNM 87304, 618 m, RV *Blake*, Sta. 2655, Little Bahama Bank; USNM 216670, RV *Albatross*, "Bahamas"; IRCZM 065:02228 472 m, RV *Johnson*, Sta. JSL-11, 24°52.2′N, 77°15.5′W, off Spanish Wells, Eleuthera; IRCZM 065:00892, 256 m, RV *Gerda*, Sta. 638, 26°05′N, 79°12′W, Bimini Banks. FLORIDA: USNM 434151, 219 m, RV *Eolis*, Sta. 330, off Sambo Reef; USNM 516445, 686 m, RV *Eolis*, Tortugas; USNM 419006, 119 m, RV *Eolis*, Sta. 100, Sand Key; USNM 419007, 382 m, *Eolis*, Sta. 340, off Fowley Light; USNM 419014, 174 m, *Eolis*, Sta. 325, off Sand Key; USNM 419010, 155 m, *Eolis*, Sta. 163, off Sand Key; USNM 419012, 165 m, *Eolis*, Sta. 319, off Western Dry Rocks; USNM 419008, 155 m, *Eolis*, Sta. 338, off Sand Key; USNM 419009, 155 m, *Eolis*, Sta. 327, off Sand Key; USNM 434152, 139 m, *Eolis*, Sta. 161, Sand Key; USNM 419011, 143 m, *Eolis*, Sta. 63, off Key West; USNM 419013, 146 m, *Eolis*, Sta. 320, off Western Dry Rocks. GULF OF MEXICO, USA: USNM 323844, 309 m, USBF Sta. 2400, off Cape San Blas, Florida; USNM 323977, 110 m, USBF Sta. 2402, off Cape San Blas, Florida; USNM 87297, 91 m, RV *Blake*, W of Florida; USNM 93998, 309 m, USBF Sta. 2400, between Mississippi Delta and Cedar Key, Florida; USNM 608531, 121 m, 100 mi off Ft. Myers, Florida; USNM 83532, Cedar Keys, Florida; USNM 323834, 309 m, USBF Sta. 2400, off Cape San Blas, Florida; USNM 323906, 203 m, USBF, off Cape San Blas, Florida; USNM 93763, 161 m, US Fish Commission Sta. 2403, between Mississippi Delta and Cedar Keys, Florida; MNHNP, 344–346 m, 28°19′N, 85°44′W; MCZ 145819, 24–35 m, 15–35 mi off Ft. Walton, Florida; Mexico: USNM 667771, 168 m, Sta. 1253, Campeche Banks off Yucatan.

RESULTS

Description: Shell small, reaching 19 mm in length and 4 mm in width [length measurements of random sample from throughout geographic range: $\bar{x} = 14.64$; sd = 2.49; range = 10.81–18.04 (n = 13)]. Shell translucent white, turreted, elongated, comprising up to 25 straight-sided whorls (figures 1, 2). Shell sculptured with 3 major, nodulose, spiral cords and 14 axial ribs per whorl (figure 4). Suture deeply impressed. Protoconch-one not seen; protoconch-two large, comprising about 3 whorls (figure 5). Protoconch-two lacking sculpture except for spiral row of minute pustules adjacent to suture and 2 very weak, spiral cords (figure 5). Pronounced sinusigeral notch present. Four to 6 juvenile whorls beneath protoconch sculptured with axial ribs only (figure 5). Subsequent early whorls with 2 beaded spiral cords per whorl that become 3 major spiral cords in later whorls (figure 6). Of these 3, first spiral cord adapical, other 2 cords separated by weaker, less nodulose spiral cord (figure 4). Body whorl constricted at siphonal canal and sculptured with 4 raised, nodulose, spiral cords and 5 or 6 smooth cords on base (figure 7). Outer lip convex and slightly pinched into posterior anal notch where it joins penultimate whorl. Aperture ovate with wide, distinct anterior canal and well-developed anal canal (figure 7).

Operculum thin, corneous, circular, externally concave, and with central nucleus; early whorls multispiral, becoming paucispiral later (figure 3).

Animal with short, wide, bilobed snout and pair of very long cephalic tentacles. Cephalic eyes large, black. Mantle edge wavy, edged with tiny papillae strongly developed at inhalant siphon. Buccal mass relatively large, bearing small pair of jaws and short taenioglossate radula.

Radula (figure 8) with about 18 rows of teeth. Rachidian tooth (figure 10) with hourglass-shaped basal plate and cutting edge of 1 large central cusp flanked on each side by 3 small denticles. Lateral tooth (figures 9, 10) wide, rhomboidal, with long lateral extension, and cutting edge comprising one sharp, tiny, inner denticle, a large pointed cusp and 4 or 5 sharp, outer denticles. Marginal teeth (figure 9) long, hook-like, with sharp tips comprising central cusp and 3 sharp, inner denticles. Inner marginal tooth with 2 small denticles on outer side; outer marginal with smooth outer edge.

Discussion: Although many authors have placed "*Cerithiopsis*" *crystallina* in the Cerithiopsidae, this classification has not really been satisfactory. Cerithiopsids are characterized by small turreted shells having well-developed, beaded, spiral sculpture, an aperture with a slight to flaring anterior notch, and a flattened, excavated shell base. They have a pleurembolic proboscis and a distinctive radula (Marshall, 1978:59–60, figs. 3, 4).

The shell of "*Cerithiopsis*" *crystallina* is not really comparable with those of cerithiopsid species. The sculpture is more nodular than beaded and more strongly spiral in composition. The base of the shell is not flattened or excavated and has a longer, wider anterior canal than those of cerithopsid species; moreover, the aperture has

a distinct anal canal and the upper lip flares into a weak notch where it joins the penultimate whorl.

The short, wide snout does not have the pleurembolic proboscis of *Cerithiopsis* species. The tiny taenioglossate radula of *C. crystallina* is close to those of members of the Cerithiidae in overall morphology (see Houbrick, 1978, 1980, 1985).

Dall (1889:254) noted the long cephalic tentacles and large, black eyes. His description of the external features of the animal agrees with my observations, but I did not find the "opercular lobe" with "several short processes on each side", which he mentioned. Dall's words seem to indicate epipodial tentacles, such as found on *Litiopa* Rang and *Alaba* H. and A. Adams species, but I found no trace of these structures. The material I examined appeared to be in good condition; consequently, I cannot explain this discrepancy.

The soft anatomy, radula, and shell of "*Cerithiopsis*" *crystallina* indicate that this species should be removed from the Cerithiopsidae, superfamily Cerithiopsacea, and transferred to the Cerithiidae, superfamily Cerithiacea. Cerithiopsids, although traditionally grouped with the cerithiids on the basis of shell morphology, are now considered as a separate superfamily (Kosuge, 1966; Marshall, 1978, 1983). They have been placed in the superorder Heterogastropoda by Kosuge (1966:297) and more recently in a new suborder, Heteroglossa, by Haszprunar (1985). Further evidence separating cerithiopsids from cerithiaceans has been presented by Healy (1983:212, 1986:195) who has discovered that their euspermatozoan morphology is quite different from that of other cerithiaceans.

Comparison of the shell and radula of *Cerithiopsis crystallina* with those of other small-shelled taxa within the Cerithiidae shows that it most closely resembles those of species in the genera *Bittium* Gray, *Argyropeza* Melvill and Standen, and *Varicopeza* Gründel. Of these three taxa, the shell shape and sculpture typical of *Bittium* species (Houbrick, 1977) does not closely match the overall morphology of *C. crystallina*, although there is some resemblance. Protoconch-two of *Argyropeza* species, as depicted by Houbrick (1979:8, fig. 2), is different from that of *C. crystallina*, as is the sculpture of the adult whorls and the aperture. Thus, *Bittium* and *Argyropeza* are best excluded as proper generic assignments. Shell characters such as the strong, nodulose spiral sculpture, deeply impressed suture, and aperture with a well-defined anal canal and posterior apertural notch all indicate a morphological resemblance to *Varicopeza*, a monotypic taxon previously known only from the Indo-Pacific and represented by *V. pauxilla* (A. Adams, 1854) (see Houbrick, 1980:528–529, figs. 1, 2). The radula of *C.*

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Figures 8–10. Radula of *Varicopeza crystallina* (Dall) from Spanish Wells, Eleuthera, Bahamas (IRCZM 065:02228). **8.** General view of radular ribbon, bar = 43 μm. **9.** Detail of half row of teeth, bar = 25 μm. **10.** Detail of rachidian and lateral teeth, bar = 10 μm.

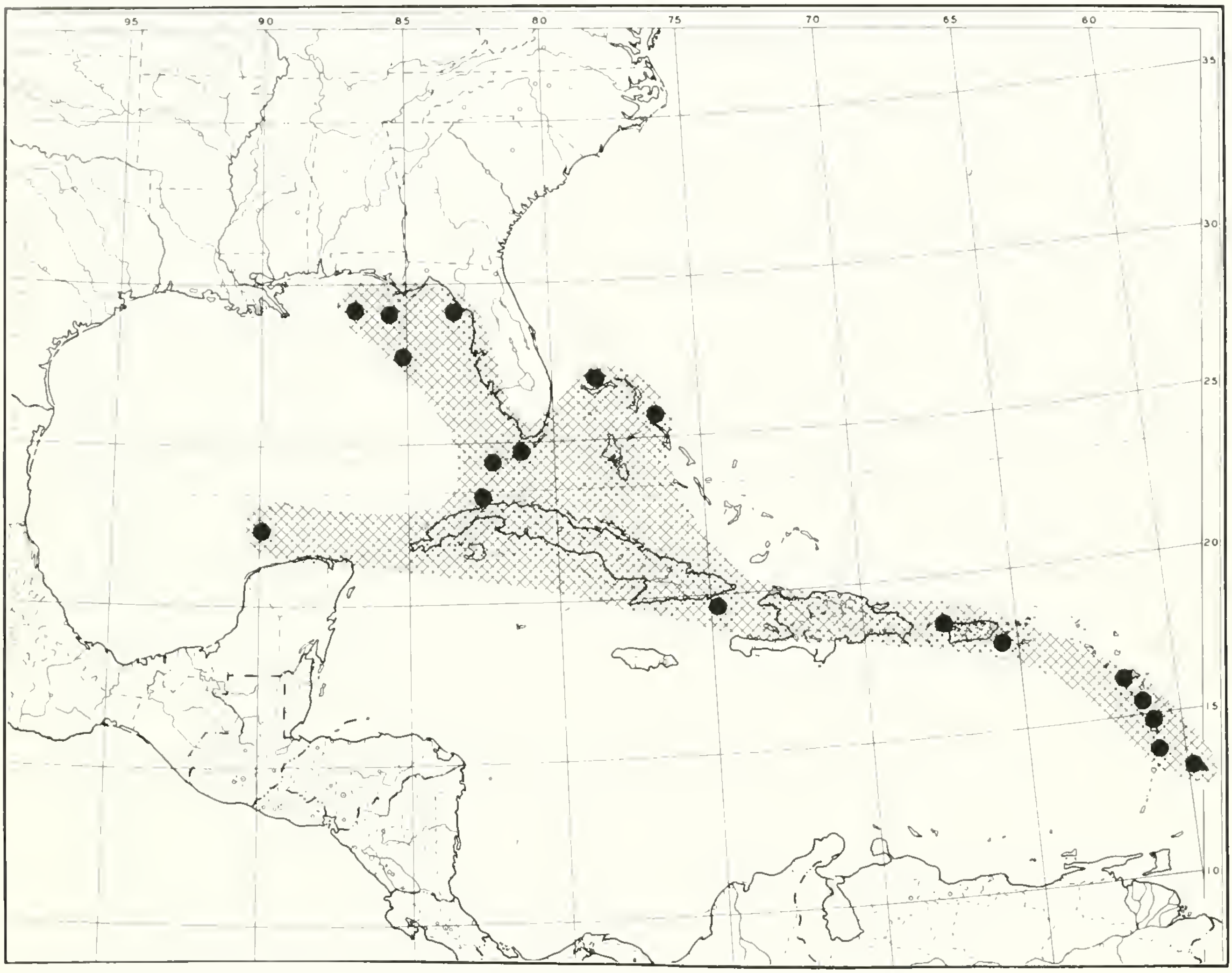

Figure 11. Geographic distribution of *Varicopeza crystallina* (Dall) based on collection data.

crystallina, particularly the hourglass-shaped rachidian tooth and the dentition and overall shape of the other teeth, is also similar to that of *Varicopeza pauxilla*. The shell of *Varicopeza pauxilla* is not as large or elongate as that of *C. crystallina* and has a more strongly defined posterior apertural notch. The operculum of the two species differs: that of *V. pauxilla* has a more eccentric nucleus and is more ovate than the operculum of *V. crystallina*. It appears that *C. crystallina* most closely resembles *Varicopeza*, and as I consider the conchological and opercular differences between the two taxa noted above to be specific ones, proposal of a new genus to accommodate *C. crystallina* is not justified. I think it best to assign this Western Atlantic species to the genus *Varicopeza*.

The genus *Varicopeza* was previously known only from a single Indo-Pacific species. The addition of *V. crystallina* to the genus adds a Western Atlantic component to the geographical distribution of this group. *Varicopeza crystallina* has a wide geographic distribution throughout the Lesser and Greater Antilles, the eastern Gulf of Mexico, and around the Florida peninsula (figure 11). Collection data indicate that it is a common offshore species having a wide bathymetric distribution ranging from 14.8 m to 1,605 m, with a mean depth of 272 m (n = 41). Nearly all lots comprised a great number of specimens. The deepest collected specimens are from the Lesser Antilles, while those from shallowest areas are from off the west coast of Florida. All specimens have come from sandy, silty bottoms and although many records are for empty shells, there were enough live-collected lots (dried animals in shells) to dismiss the possibility that this species occurs in significantly different bathymetric ranges than indicated. Specimens (empty shells) have been found on the beach at Cedar Keys, Florida

CONCLUSIONS

Synonymy: The following synonymy summarizes the taxonomic decisions reached in this paper. A more complete definition of the genus *Varicopeza* is found in Houbrick (1980:525–526).

Family **Cerithiidae** Fleming, 1822
Genus *Varicopeza* Gründel, 1976

Varicopeza crystallina (Dall, 1881)

Cerithiopsis ? crystallina Dall, 1881:89. Holotype: MCZ 7395, figured type and one paratype; type-locality: RV *Blake*, Sta. 2, off Morro Light, N of Havana, Cuba—also Barbados; here restricted to off Morro Light, N of Havana, Cuba, 1889:254, pl. 20, fig. 3.

Cerithiopsis crystallinum Dall. Abbott, 1974:109, fig. 1049G; Dall and Simpson, 1901:424; Warmke and Abbott, 1962: 75; Rice and Kornicker, 1965:119, pl. 2, fig. 9; Boss *et al.*, 1968:95.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. New York, 663 p., 24 pls., 6405 figs.

Adams, A. 1854. A monograph of *Cerithidea*, a genus of Mollusca, with descriptions of several new species, from the collection of Hugh Cuming, Esq.: to which are added descriptions of two new species of *Colina*, and one of *Donax*. Proceedings of the Zoological Society of London 22:83–87.

Boss, K. J., J. Rosewater, and F. A. Ruhoff. 1968. The zoological taxa of William Healy Dall. Bulletin of the U.S. National Museum No. 287:427 p.

Dall, W. H. 1881. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and in the Caribbean Sea, 1877–1879, by the U.S. Coast Steamer "Blake". Preliminary report on the Mollusca. Bulletin of the Museum of Comparative Zoology, Harvard 9: 33–144.

Dall, W. H. 1889. Reports of the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer "Blake". Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. Report on the Mollusca. Part 2. Gastropoda and Scaphopoda. Bulletin of the Museum of Comparative Zoology, Harvard 18:1–492, pls. 10–40.

Dall, W. H. and C. T. Simpson. 1901. The Mollusca of Porto Rico. Bulletin of U.S. Fish Commission for 1900 1:351–524, pls. 53–58.

Fleming, J. 1822. The philosophy of zoology or a general view of the structures, functions, and classifications of animals, etc., 2 vols. Edinburgh, no pagination.

Forbes, E. and S. Hanley. 1850–51. A history of British Mollusca and their shells, Vol. 3. Van Voorst, London, 616 p.

Gray, J. E. 1847. The classification of the British Mollusca by N. E. Leach, M.D. Annals and Magazine of Natural History 20:267–273.

Gründel, J. 1976. Zur Taxonomie und Phylogenie der *Bittium*-Gruppe (Gastropoda, Cerithiacea). Malakologische Abhandlungen Staatliches Museum für Tierkunde in Dresden 5(3):33–59, 2 pls., 17 figs.

Haszprunar, G. 1985. The Heterobranchia—a new concept of the phylogeny of the higher Gastropoda. Zeitschrift für Zoologische Systematik und Evolutionsforschung 23(1):15–37.

Healy, J. M. 1983. Ultrastructure of euspermatozoa of cerithiacean gastropods (Prosobranchia: Mesogastropoda). Journal of Morphology 178:57–75.

Healy, J. M. 1986. Ultrastructure of paraspermatozoa of cerithiacean gastropods (Prosobranchia: Mesogastropoda). Helgolander Meeresuntersuchungen 40:177–199.

Houbrick, R. S. 1977. Reevaluation and new description of the genus *Bittium* (Cerithiidae). The Veliger 20(2):101–106.

Houbrick, R. S. 1978. The family Cerithiidae in the Indo-Pacific, Part 1: the Genera *Rhinoclavis*, *Pseudovertagus*, *Longicerithium*, and *Clavocerithium*. Monographs of Marine Mollusca No. 1:130 p., 98 pls.

Houbrick, R. S. 1979. Review of the deep sea genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae). Smithsonian Contributions to Zoology No. 321:30 p., 12 pls.

Houbrick, R. S. 1980. Reappraisal of the gastropod genus *Varicopeza* Gründel (Cerithiidae: Prosobranchia). Proceedings of the Biological Society of Washington 93(3): 525–535.

Houbrick, R. S. 1985. Monograph of the genus *Clypeomorus* (Cerithiidae, Prosobranchia). Smithsonian Contributions to Zoology No. 403:131 p., 62 pls.

Kosuge, S. 1966. The family Triphoridae and its systematic position. Malacologia 4(2):297–324.

Marshall, B. A. 1978. Cerithiopsidae (Mollusca: Gastropoda) of New Zealand and a provisional classification of the family. New Zealand Journal of Zoology 5:47–120.

Marshall, B. A. 1983. A revision of the Recent Triphoridae of southern Australia. Records of the Australian Museum, Supplement 2:119 p., 33 figs.

Rice, W. H. and L. Kornicker. 1965. Mollusks from the deeper waters of the northwestern Campeche Bank, Mexico. Publications of the Institute of Marine Science, Texas 10:108–172.

Warmke, G. and R. T. Abbott. 1961. Caribbean seashells. Narberth, PA, 346 p., 44 pls.

Watson, R. B. 1884–86. Report on the Scaphopoda and Gasteropoda collected by H.M.S. *Challenger* during the years 1873–1876. *In:* Report on the scientific results of the voyage of the H.M.S. *Challenger* during the years 1873–76 15(42):756 p., 53 pls.

Identity and Status of *Philomycus pennsylvanicus* Pilsbry, 1894 (Gastropoda: Pulmonata: Philomycidae)

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ABSTRACT

The nomenclatural history of *Philomycus pennsylvanicus* Pilsbry, 1894 is reviewed. As the original specimens were lost and their description was incomplete, two field trips were conducted to locate the population from which the specimens were collected. The results of this fieldwork and a study of the International Code of Zoological Nomenclature support two conclusions: (1) *Philomycus pennsylvanicus* is a *nomen nudum* and (2) the slug that Pilsbry began to describe is probably what is now known as *Megapallifera mutabilis* (Hubricht, 1951).

INTRODUCTION

The name *Philomycus pennsylvanicus* was cited by Pilsbry (1894) for "A maculated species . . .", an extremely cryptic description. A "Full description . . ." was to be published at a later date. Subsequent usage in faunal lists or descriptive papers was limited to Sterki (1907), Dall (1916), and Clapp (1920). In his monograph of North American land mollusks, Pilsbry (1948:767) transferred the name to the genus *Pallifera*, and explained the lack of the promised detailed description, because of ". . . a local flood . . ." which destroyed the specimens. Pilsbry (1948) also noted that "It is practically a nude name."

The original collection by Witmer Stone was from York Furnace, York County, Pennsylvania. Fieldwork to resample this population and lab work to determine its identity are reported below.

MATERIALS AND METHODS

Two field trips were conducted to the town of York Furnace, York County, Pennsylvania (ca. 76°23′18″W, 39°52′25″N) (figure 1), the locality given by Pilsbry (1894). Specimens were collected from trees, logs, under loose bark, and in the litter around the bases of trees. Data collected included length (live specimens), mantle pattern, and the appearance of the jaw and reproductive system. Dissected specimens were drowned first in distilled water. All material was preserved in 70% ethanol.

RESULTS

A total of 22 slugs were collected on May 22, 1984, after a rainy night. Dissection revealed that all but one of these specimens were attributable to the genus *Philomycus* (presence of dart sac and dart). The reproductive system of the one specimen was not fully developed, but the slug did have a ribbed jaw and was therefore identified as a species of *Pallifera*.

An additional 36 slugs were found on July 18, 1984, also after a night of rain. The mantle pattern on five of these slugs was different from that of the others. Dissection demonstrated that all five lacked a dart sac and dart; the other 31 were all species of *Philomycus* (dart and dart sac present). One of the five specimens measured 30 mm in length (crawling), the others were larger (four specimens, average length crawling 51 mm, range 45–55 mm). All specimens were mature, *i.e.*, had fully developed reproductive systems.

Voucher material, three specimens of *Philomycus carolinianus* and one specimen of *Pallifera mutabilis* has been deposited in the United States National Museum (USNM 853181 and 853182).

DISCUSSION

The International Code of Zoological Nomenclature (1985) Chapter IV, Article 12 states, "To be available every new scientific name published before 1931 must satisfy the provisions of Article 11 and must be accompanied by a description or a definition, of the taxon that it denotes, or by an indication." In addition, Article 10(b) states, "If publication of the data relating to a new nominal taxon or a nomenclatural act is interrupted and continued at a later date, the name or nomenclatural act becomes available only when it satisfies all the relevant provisions of Articles 10 to 20." Pilsbry stated (1894) that he would publish a "Full description with anatomical details . . ." at a later date. Clearly, publication was interrupted because he intended to publish at a later date, data ". . . relating to a new nominal taxon . . .". Because the name did not become available, Pilsbry created a

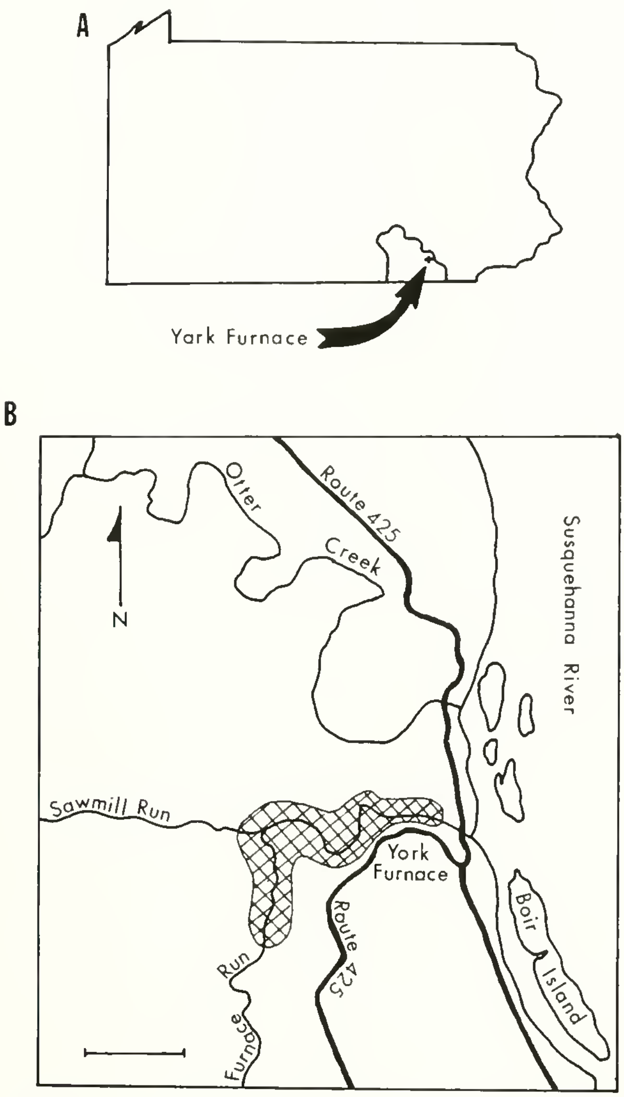

Figure 1. A. The location of York Furnace in York County, Pennsylvania. B. The York Furnace area, the cross-hatching represents the search area. Scale bar equals 0.5 km.

nomen nudum which has no standing in zoological nomenclature.

Comparison of the dart-less slugs collected at York Furnace during this study with the descriptions of the species of *Pallifera* and *Megapallifera* resulted in the following identifications. The larger specimens were *M. mutabilis* (Hubricht, 1951) (confirmed by L. Hubricht, personal communication, August 31, 1984); the smaller specimen was *Pallifera fosteri* Baker, 1939.

Pilsbry (1894) described *Philomycus pennsylvanicus* as "A maculated species having the jaw strongly ribbed. It is smaller and less distinctly marked than *P. carolinianus*" (length crawling 70–100 mm). Pilsbry was familiar with *Pallifera dorsalis*, then called *Philomycus dorsalis* (length crawling 20–25 mm). If *P. pennsylvanicus* was small, *i.e.*, 30 mm long, it would seem likely that Pilsbry would have compared it to *Pallifera dorsalis*. Smaller than *Philomycus carolinianus* then probably meant closer to 70 mm long rather than 25 mm, *i.e.*, closer to the size of *Megapallifera mutabilis* (length crawling *ca.* 50 mm), not *Pallifera fosteri* (length crawling *ca.* 30 mm).

The results of this study support two conclusions. One, *Philomycus pennsylvanicus* is a *nomen nudum* and therefore must be dropped from the literature and should not appear in any future synonymy. Two, it appears likely that the slug Pilsbry described was what is now known as *Megapallifera mutabilis* (Hubricht, 1951).

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LITERATURE CITED

Baker, F. C. 1939. Fieldbook of Illinois land snails. Illinois Natural History Survey Manual 2:133–134. Urbana, Illinois.

Clapp, W. F. 1920. The shell of *Philomycus carolinianus* (Bosc). The Nautilus 33(3):83–89.

Dall, W. H. 1916. Shells of Mt. Monadnock, N.H. The Nautilus 30:57–58.

Hubricht, L. 1951. Three new land snails from eastern United States. The Nautilus 65(2):57–59.

International Commission of Zoological Nomenclature. 1985. International Code of Zoological Nomenclature, 3rd ed. London, 338 p.

Pilsbry, H. A. 1894. Critical list of mollusks collected in the Potomac Valley. Proceedings of the Academy of Natural Sciences of Philadelphia for 1894:11–31.

Pilsbry, H. A. 1948. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monographs No. 3, Vol. II, Part 2.

Sterki, V. 1907. A preliminary catalogue of the land and fresh-water Mollusca of Ohio. Proceedings of the Ohio State Academy of Sciences Vol. IV, Part 8, Special Papers No. 12:367–402.

The Diet and Feeding Behavior of *Cadulus tolmiei* Dall, 1897 (Scaphopoda: Siphonodentalioida)

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ABSTRACT

Specimens of *Cadulus tolmiei* and sediment samples were obtained from Numukamis Bay, Barkley Sound, off Vancouver Island, British Columbia. The shell length and oral aperture diameter were measured, and the scaphopods dissected to remove gut contents. Live and dead prey items were recorded, and foraminiferans identified to genera. Sediment samples were analyzed for potential prey. Chi square tests showed significant differences between the relative abundances of organisms in the buccal pouches and the sediment, and between the relative abundances of live and dead organisms within the buccal pouches. Selective indices show *C. tolmiei* to feed preferentially on living foraminiferans, particularly *Uvigerina* sp. The feeding behavior of this cadulid is similar to that of dentalioid scaphopods.

INTRODUCTION

The class Scaphopoda is a very uniform group within Mollusca, characterized by specialized habits and simplified structures (Morton & Yonge, 1964). Scaphopods are detritivores and micro-carnivores, living in the sand with their shell apices above the substrate (Morton, 1967). The shell is usually oriented with its concave side upward (figure 1).

Palmer (1974) divided the Scaphopoda into the orders Dentalioida and Siphonodentalioida, which can be distinguished on the basis of external features. The Dentalioida have elongated conical shells and a conical foot. The Siphonodentalioida have a vermiform foot with a crenulated pedal disc, and are generally smaller than dentalioids (Pelseneer, 1906; Palmer, 1974).

Scaphopods burrow and construct a feeding cavity wherein the captacula probe the cavity walls (Gainey, 1973) and substrate, and detect and capture live foraminiferans and other prey (Morton, 1959; Gainey, 1973; Bilyard, 1974). Dentalioid epipodial lobes may dislodge and waft sediment toward the oral aperture, where the captacula probe it (Dinamani, 1963). When food is absent, scaphopods burrow to a new location (Gainey, 1973).

Dinamani (1963) observed *Dentalium conspicuum* Melvill collecting and conveying particles along its captacula by ciliary action. These particles were whisked onto the captaculum by the cilia on the bulbous tip and transported along the filament to the mouth by ciliary action. Morton (1959) suggested that *D. entalis* Linné may use captacular alveoli as suction cups to capture foraminiferans. Gainey (1973) observed *D. eboreum* Conrad and *D. pseudohexagonum* Henderson probing into the substrate with their feet to form feeding cavities (figure 1, fc). The captacula then browsed along the cavity walls and conveyed small particles to the mouth. Bilyard (1974) showed that *D. entale stimpsoni* Henderson feeds selectively on living foraminiferans and organic material, and rejects dead foraminiferans and inorganic material. There have been few studies on siphonodentalioids. Davis (1968) described the captacular behavior of *Cadulus quadridentatus* Dall, but did not observe feeding. Rokop (1977) reported a seasonal reproductive cycle in *C. californicus* Pilsbry and Sharp.

Cadulus tolmiei is a common deepwater siphonodentalioid occurring in Barkley Sound, off the western coast of Vancouver Island, British Columbia. The feeding behavior of this species is described and compared to that of dentalioid scaphopods. The diet of *Cadulus tolmiei* and the selection of particular prey items are reported.

MATERIALS AND METHODS

Specimens of *Cadulus tolmiei* were dredged from two sites in Numukamis Bay on June 22, 1984. Site 1 (48°53.70′N, 125°00.83′W to 48°54.01′N, 125°02.98′W, in 139–199 m) yielded 26 specimens; site 2 (48°53.80′N, 125°03.12′W to 48°53.77′N, 125°03.84′W, in 157–183 m) yielded 61 specimens (voucher specimens USNM 859073). A thermometer was inserted into the samples immediately upon collection to determine the bottom sediment temperature. Temperatures at site 2 averaged 8.9 ± 0.4 °C. No sediment was obtained at site 1.

Twenty-four specimens from site 1 and 11 specimens from site 2 were preserved in 37% isopropyl alcohol containing Rose Bengal. Shell lengths and oral aperture widths were measured, and the specimens dissected. All prey items were removed from the buccal pouches, live (stained) and dead (unstained) prey items recorded, and

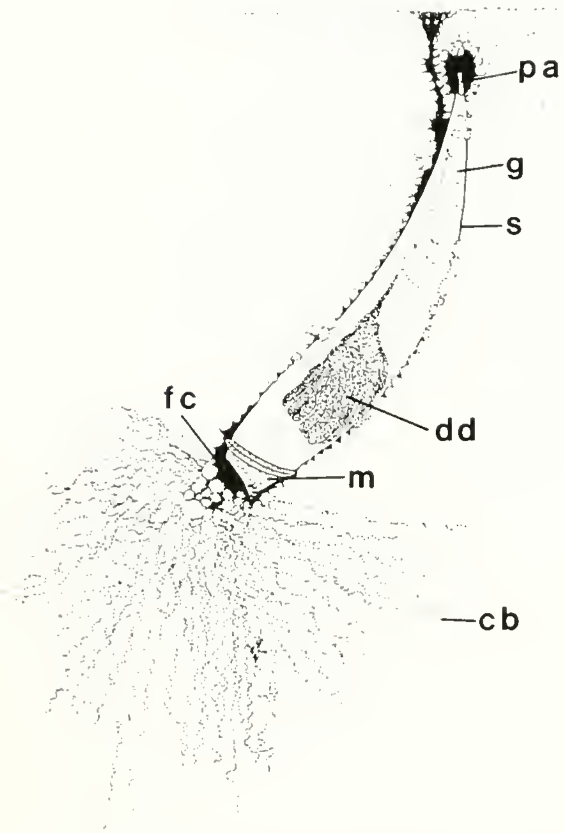

Figure 1. *Cadulus tolmiei* in sediment, showing orientation cb, captacular burrow; dd, digestive diverticula; fc, feeding cavity; g, gonad, m, mantle; pa, posterior appendix; s, shell.

prey maximum lengths measured. Foraminiferans were identified to genus using the keys in Cushman (1959).

Sediment samples were immediately preserved in Rose Bengal–isopropanol solution, sieved to 63 μm and examined under a dissecting microscope. All stained potential prey items were counted and collected.

A linear regression (Schefler, 1969) of *C. tolmiei* oral aperture width *vs.* live prey item length was plotted and the correlation coefficient calculated. Chi square tests (Siegel, 1956) were used to determine if there were significant differences between the prey items in the buccal pouches and in the sediment, and between the live and dead prey items in the buccal pouches. Selective indices (Bilyard, 1974), the ratios of percent organisms in the buccal pouches to the percent organisms in the sediment, were calculated for the major prey categories. Indices greater than 1.0 indicate positive selectivity, values less than 1.0 indicate negative selectivity (Bilyard, 1974).

Additional sediment was sieved through a 1 mm screen to remove macro-invertebrates, and kept in plastic, mesh-sided containers in circulating seawater (9.6 ± 0.2 °C). These samples were further sieved through 275 μm, 180 μm, and 63 μm screens to retrieve foraminiferans for use as prey in feeding observations. Living *Cadulus tolmiei* were attached to glass slides with rubber bands and placed about 1 mm above the substrate in a small glass tank filled with sediment and seawater (figure 2). Temperature was maintained at 13.2 ± 0.8 °C. Specimens were backlit to reveal internal activity through the translucent shell. Foraminiferans were placed in the tanks and feeding observed through a horizontally mounted dissecting microscope.

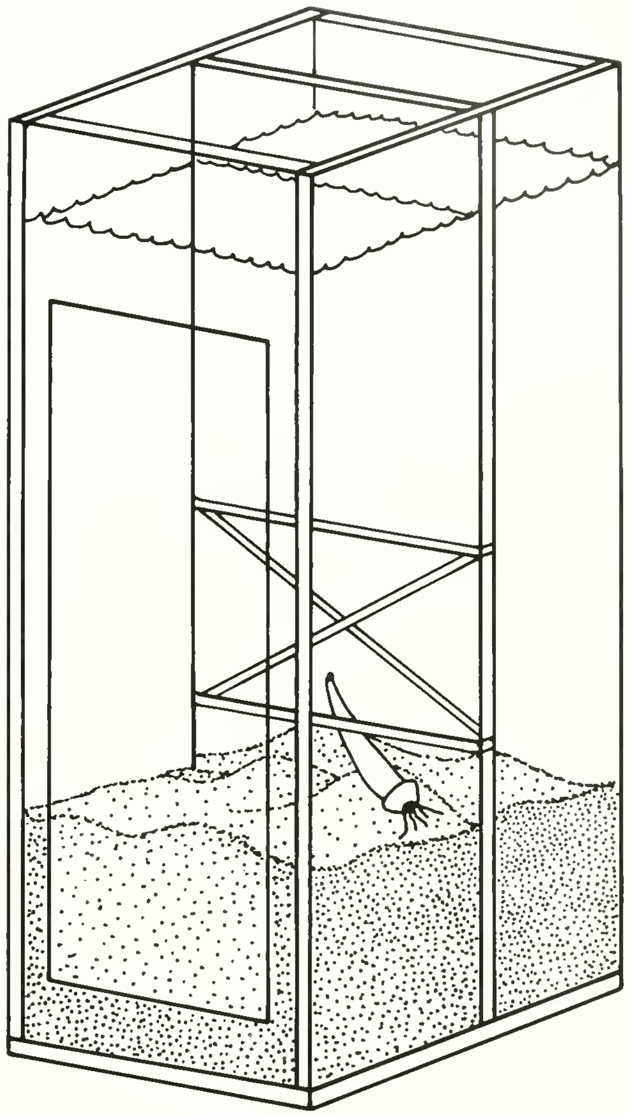

Figure 2. Observation tank constructed from 2 × 8 cm glass slides. Scaphopod is attached to slide by rubber band.

RESULTS

Living and dead organisms taken from the buccal pouches of *Cadulus tolmiei* were identified, counted, and are listed in table 1. The site 2 sediment sample was composed mostly of silty fecal pellets. Nematodes, annelids and dead centric diatoms were common. The foraminiferans *Bulimina* sp., *Uvigerina* sp., *Bolivina* sp., *Quinqueloculina* sp., and *Rheophax* sp. were present in the

Table 1. Buccal pouch contents of 26 *Cadulus tolmiei*.

Live prey items	Number Dead	Live	Total
Foraminifera			
Bulimina sp.	29	18	47
Uvigerina sp.	2	24	26
Bolivina sp.	5	1	6
Truncatulina sp.	4	2	6
Discorbis sp.	1	2	3
Globigerina sp.	1	2	3
Nonionella sp.	1	0	1
Unidentified foraminiferan	1	0	1
Foraminiferan fragments	6	1	7
Uvigerina sp. fragments	3	4	7
Bulimina sp. fragments	2	2	4
Mollusca			
Juvenile Bivalves	1	1	2
Eggs			
Thick shelled eggs	2	27	29
Thin shelled eggs	3	1	4
Egg shell	1	0	1
Inorganic material			
Detritus	6	0	6
Other			
Unidentified Test	0	1	1
Total	68	86	154

Table 2. Live potential prey in sediment.

Prey items	Prey per ml
Foraminifera	
Bulimina sp.	0.6
Uvigerina sp.	0.1
Bolivina sp.	0.1
Nonionina sp.	0.1
Mollusca	
Juvenile Bivalves	0.1
Eggs	
Thick shelled eggs	0.6
Thin shelled eggs	0.1

Total number of prey items: 90

Total volume of sediment examined: 58.6 ml

Table 3. Chi square test comparing live prey in sediment and buccal pouches.

Live prey items	Number in sediment	Number in buccal pouches	Total
Bulimina sp.	33	51	84
Uvigerina sp.	4	33	37
Eggs	39	34	73
Others	14	36	50
Total	90	154	244

$\chi^2_{(\alpha = 0.001,\ 3\ df)} = 16.27$

$\chi^2_{calculated} = 20.75$

Table 4. Chi square test comparing dead and live prey within the buccal pouches.

Prey items	Number dead	Number live	Total
Bulimina sp.	31	20	51
Uvigerina sp.	5	28	33
Eggs	6	28	34
Others	26	10	36
Total	68	86	154

$\chi^2_{(\alpha = 0.001,\ 3\ df)} = 16.27$

$\chi^2_{calculated} = 38.21$

Table 5. Selective index of percent prey in buccal pouches and in sediment.

Prey items	Percent in sediment	Percent in buccal pouches	Selective index
Bulimina sp.	36.7	30.5	0.8
Uvigerina sp.	4.5	16.9	3.8
Bolivina sp.	6.7	3.9	0.6
Thick shelled eggs	40.0	18.8	0.5
Thin shelled eggs	3.4	2.6	0.8
Juvenile bivalves	7.8	1.3	0.2

sediment sample. *Rheophax* sp. was common, as were tests of dead *Uvigerina* sp. and *Bulimina* sp. Tests of *Quinqueloculina* sp. were less common. *Rheophax* sp. was the only arenaceous foraminiferan found. Table 2 lists the potential prey items in this sediment sample.

Chi square tests indicated significant differences between the distribution of prey items in the buccal pouches *vs.* the sediment (table 3) and between living and dead prey items in the buccal pouches (table 4). Live *Uvigerina* sp. were strongly selected. Dead *Bulimina* sp., *Bolivina* sp., and thin shelled eggs were occasionally selected, but few live individuals were ingested. Live thick-shelled eggs were selected over dead ones. Living and dead juvenile bivalves were avoided (tables 5 and 6). The linear regression of prey size versus oral aperture width is shown in figure 3. The slope is −25.3; the correlation coefficient (−0.02) is insignificant.

The feeding behavior of 40 individuals was observed. After burrowing, each animal slowly extended and retracted its foot with the pedal disc invaginated. This movement created a small feeding cavity (figure 1, fc).

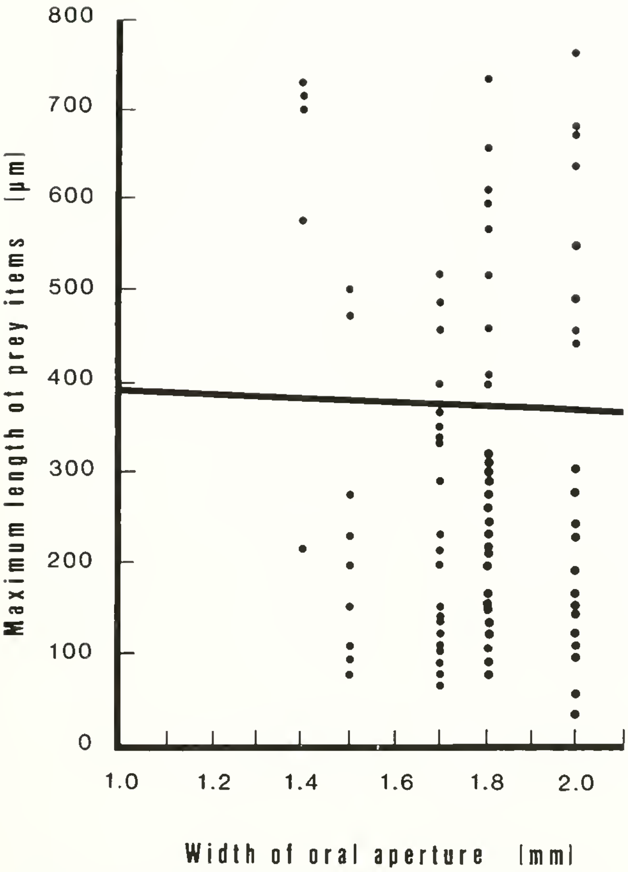

Figure 3. Plot of oral aperture size versus prey item size. Linear regression, $Y = 275.9 + (-25.3)(X - 1.8)$.

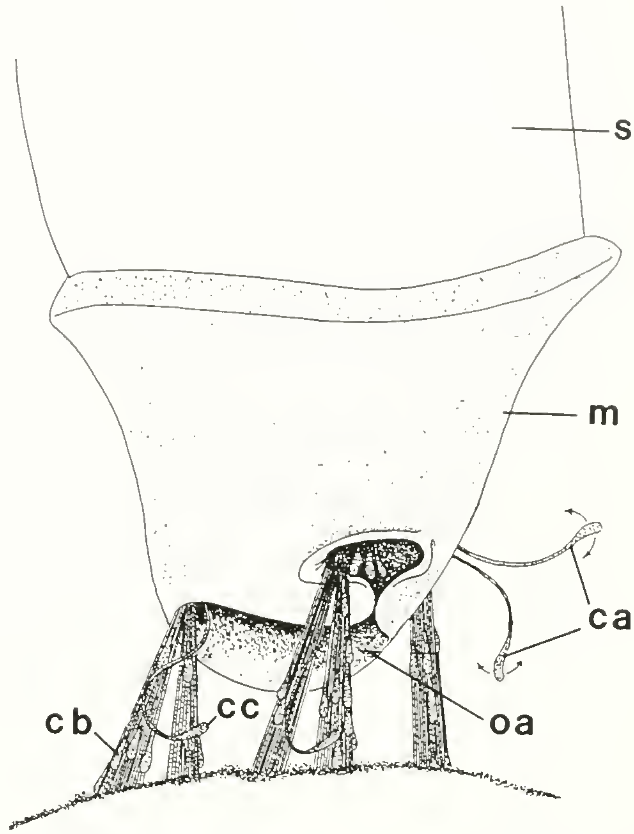

Figure 4. *Cadulus tolmiei* feeding. ca, captacula flexing tip; cb, captacula crawling along other captacula; cc, retracting captacula; m, mantle; oa, oral aperture; s, shell.

Within the shell, the proboscis and captacula were lowered close to the anterior aperture (figure 4, oa). A few captacula slowly emerged from the opening, and their tips flexed and bent (figure 4, ca). After these captacula entered the substrate, they were followed by more captacula crawling with their cilia along straight, taut, captacular filaments (figure 4, cb). In buried specimens, captacula and captacular burrows (figure 1, cb) radiated from the feeding cavity (figure 1, fc).

Sediment was moved along straight and sinuous captacula. Some particles fell from the filaments, while lumps of sediment blocked other conveyed particles. Ciliary movement on the captacula was clearly visible with transmitted light. Captacula entered the substrate with little resistance, with sediment particles being displaced by ciliary action. Little conveying was seen after the captacula were buried.

Table 6. Selective index of percent dead and live prey in buccal pouches.

Prey items	Selective index (dead)	Selective index (live)
Bulimina sp.	1.2	0.6
Uvigerina sp.	0.6	6.2
Bolivina sp.	1.1	0.2
Thick shelled eggs	0.1	0.8
Thin shelled eggs	1.3	0.4
Juvenile bivalves	0.2	0.2

Some captacula were retracted into the oral aperture (figure 4, oa) without any visible material, yet their tips were bent backwards (figure 4, cc). Other captacular bulbs were wrapped around large particles, or were entwined and pulled sediment toward the oral aperture. Some captacula separated and pulled apart the lumps of sediment while others probed the broken lumps of sediment. The passing of small objects from captaculum to captaculum, the extension of the proboscis toward the captacular lobes, and the opening and closing of the mouth were observed through the shell. Although no cilia or furrows were observed on the foot, small particles of sediment were transported into the mantle cavity when the foot was retracted.

DISCUSSION

Linear regression analysis showed no relationship between oral aperture diameter and prey size in *Cadulus tolmiei*. These variables were also uncorrelated in *Dentalium* (Bilyard, 1974).

Chi square tests and selectivity indices show strong selection for live *Uvigerina* sp. Live *Reoplax* sp. were common in sediment, but were rejected, possibly because their quartz grain tests lack organic material (Bilyard, 1974). Thick shelled eggs were organic, and showed a high selective index (Bilyard, 1974), with more live eggs selected than dead eggs. Ganglia in the captacular bulb (Morton, 1959; Gainey, 1973) may chemically detect live foraminiferans, and reject empty tests (Bilyard, 1974). Nematodes and annelids were never captured, presumably because they were able to escape (Bilyard, 1974). Diatom tests and *Quinqueloculina* sp. were not selected, probably because no living individuals were present in the sediment. The negative selection of juvenile bivalves was puzzling, especially since they were strongly selected by *Dentalium* (Bilyard, 1974).

The feeding behavior of *Cadulus tolmiei* is similar to that reported for dentalioids. Similarities include feeding cavity construction (Dinamani, 1963; Gainey, 1973); captacular tip flexure, captacular enclosure of objects, and passing of material from captaculum to captaculum within the shell (Gainey, 1973); captacular entwining (Dinamani, 1964); and captacular sediment pulling (Gainey, 1973). Observations of captacula crawling along other, taut captacula are unique.

Although ciliary conveyance of particles along captacula has been observed in other species (Dinamani, 1963; Gainey, 1973) it is not an efficient method for gathering food because particles fall off and block other particles. Captacular filaments of *Cadulus tolmiei* are about 30 μm in diameter, too small to convey *Uvigerina* sp. (482 μm long). Captacular cilia are likely used primarily for extension (Morton, 1959; Davis, 1968). The large size of prey items, small amount of detritus in the buccal pouches, and the relatively large radula suggest that *C. tolmiei* is a micro-carnivore.

When feeding, the foot of *Dentalium* makes strong rhythmic movements and sucks particles into the mantle cavity (Gainey, 1973). This behavior was not observed when *C. tolmiei* fed, although sediment was sucked into the mantle cavity by the retracting foot during burrowing. *Cadulus tolmiei* may also capture foraminiferans with its pedal disc (Shimek, personal communication).

Cadulus tolmiei is common in deep water in Barkley Sound, where it lives in a silty fecal pellet substrate. Observations have shown it to be a micro-carnivore selectively feeding upon live calcareous foraminiferans, particularly *Uvigerina* sp. Its behavior is similar to that reported for dentalioids, with only minor differences in captacular extension. Feeding behavior appears to be homogeneous in the class Scaphopoda.

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LITERATURE CITED

Bilyard, G. R. 1974. The feeding habits and ecology of *Dentalium entale stimpsoni* Henderson. The Veliger 17(2): 126–138.

Cushman, J. A. 1959. Foraminifera. Their classification and economic use. Harvard University Press, Cambridge, MA, 605 p.

Davis, J. D. 1968. A note on the behavior of the scaphopod, *Cadulus quadridentatus* (Dall) 1881. Proceedings of the Malacological Society of London 38:135–138.

Dinamani, P. 1963. Burrowing behavior of *Dentalium*. Biological Bulletin 26(1):28–32.

Dinamani, P. 1964. Feeding in *Dentalium conspicuum*. Proceedings of the Malacological Society of London 36(1): 1–5.

Gainey, L. F., Jr. 1973. The use of the foot and the captacula in the feeding of *Dentalium* (Mollusca: Scaphopoda). The Veliger 15(1):29–34.

Morton, J. E. 1959. The habits and feeding organs of *Dentalium entalis*. Journal of the Marine Biological Association of the United Kingdom 38:225–238.

Morton, J. E. 1967. Mollusca Hutchison University Library, London, p. 108–109.

Morton, J. E. and C. M. Yonge. 1964. Chapter I. Classification and structure of the Mollusca. *In:* Wilbur, K. M. and C. M. Yonge (eds.). Physiology of Mollusca, Vol. 1. Academic Press, New York, p. 32–33

Palmer, C. P. 1974. A supraspecific classification of the scaphopod Mollusca. The Veliger 172:115–123.

Pelseneer, P. 1906. Chapter IV. The Scaphopoda. *In:* Lankester, E. R. (ed.). A treatise on zoology. Part V. Mollusca. Adam and Charles Black, London, p. 197–204.

Rokop, F. J. 1977. Seasonal reproduction of the brachiopod *Frieleia halli* and the scaphopod *Cadulus californicus* at bathyal depths in the deep sea. Marine Biology 43:237–246.

Schefler, W. C. 1969. Statistics for biological sciences. Addison-Wesley Publishing Company, Don Mills, Ontario, p. 150–154.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, Toronto, p. 104–107.

Sympatric Species of *Nautilus* (*N. pompilius* and *N. scrobiculatus*) in the Admiralty Islands, Papua New Guinea

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ABSTRACT

Deep-water trapping off Manus, Papua New Guinea, has produced the first known living specimens of *Nautilus scrobiculatus* Lightfoot, 1786, a species previously known only from rare drift shells, with the exception of a single necrotic individual (Willey, 1902). The present report also represents the first record of sympatric species of *Nautilus*; *N. scrobiculatus* occurs with *N. pompilius* in a 1:7 ratio. At all other sites where *Nautilus* has been obtained (including three in Papua New Guinea) only one species (generally *N. pompilius* Linnaeus, 1758) has been reported. The shell of *N. scrobiculatus* has a dense, golden, moss-like periostracal covering, giving the living animal a shaggy appearance that is unique among living species of *Nautilus*. Additional soft-part differences include a rough-textured hood and brownish tissue pigmentation.

INTRODUCTION

The rarest and perhaps most distinctive species of *Nautilus*, *N. scrobiculatus* Lightfoot, 1786, was named two centuries ago from a shell in the collection of the Duchess of Portland. Reverend Lightfoot's description of the species was minimal, and the source of the shell was merely cited as "New Guinea, very rare . . . ."

With one exception, knowledge of the range and habitat of this enigmatic species has been limited to finds of drifted shells, which were most often obtained from the Solomon Islands and Papua New Guinea. Willey reported (1902:744):

> . . . I was therefore very pleased to come into the possession of a single mutilated specimen of *N. umbilicatus* [= *N. scrobiculatus*] accompanied by its shell, which had been picked up from the surface of the sea, not far from Milne Bay in British New Guinea, and to find that this species differed notably from its congeners by the character of the hood, the gibbosities of which have the form of flat-topped angular areas separated by deep grooves, producing a pronounced tessellated appearance.

Willey's find was never duplicated, but *N. scrobiculatus* continued to hold more than ordinary interest. Many features of its shell are unique by comparison to the other extant species, including the prominent, square-shouldered umbilicus, the distinctive color markers, the heavy scrobiculate ornament, and, as Willey had pointed out, this appeared to be the only living species of *Nautilus* that exhibited differences in the soft parts as well as the shell. Stenzel (1964:87) remarked that the shell of *N. scrobiculatus* ". . . differs in so many features from the others that it is logical to place it in a separate subgenus."

The present report comprises the first account of living specimens of *Nautilus scrobiculatus*. It is also the first record of the sympatric occurrence of two species of *Nautilus*. The specimens described here were obtained off the south coast of Manus Island, in the Admiralty Islands of the Bismarck Archipelago, Papua New Guinea, in 1984 and 1985. This site was chosen because drifted shells of both *Nautilus pompilius* and *N. scrobiculatus* were reported to be fairly common on the beaches within the island complex (Knight, 1975).

MATERIALS AND METHODS

Baffle-style traps *ca.* 1 × 1 × 2 m, covered with wire mesh and baited with tuna, were typically set for one to three nights at *ca.* 200–400 m depths against the face of fringing reefs around Ndrova Island and the Fedarb Islands (referred to locally as Komuli), just southeast of the main island, Manus (figure 1). Following trapping, each animal was weighed, measured, sexed, inspected for epizoans and evidence of predation, injury, and shell repair, then photographed, and released by diver or retained for study (following techniques of Saunders & Spinosa, 1978, and Saunders, 1983). A battery-powered remote 35 mm deep-water camera (Jay-Mar Engineering, 1910 Milan Place, San Pedro, CA) was used to obtain photosequences showing the animals in their natural habitat, following techniques used successfully in Palau (Saunders, 1984). A total of 15 photosequences, each spanning 9 or 18 hr periods, with photographs taken at 15 or 30 min intervals was obtained at depths of 145–300 m.

Specimens of *N. scrobiculatus* and of *N. pompilius* from Manus, as well as from sites near Kavieng, Lae, and Port Moresby, are reposited at the Smithsonian In-

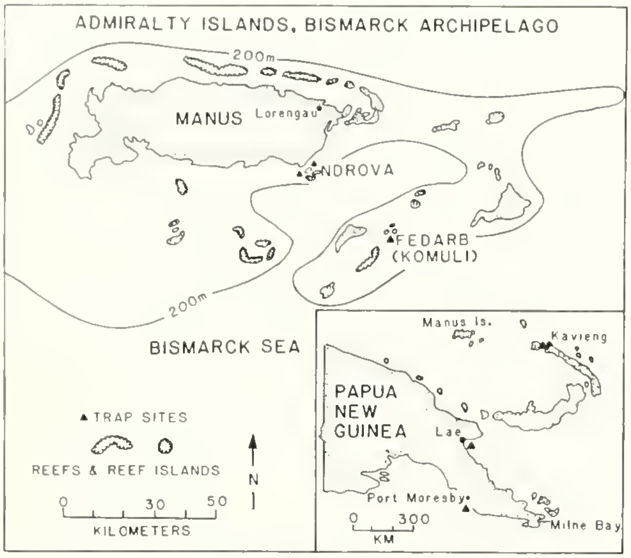

Figure 1. Location map of Manus region, Papua New Guinea. Both *Nautilus pompilius* and *N. scrobiculatus* were trapped off Ndrova and off Komuli (Fedarb Islands). Note that *N. pompilius*, but not *N. scrobiculatus*, was also obtained at Kavieng, Lae, and Port Moresby (see inset).

stitution, National Museum of Natural History, Washington, DC (USNM 816504–816505, 816702), the American Museum of Natural History, New York (AMNH 43261, 43262), and at the Natural Science Resource Centre, Biology Department, University of Papua New Guinea, Port Moresby (NSRC 502–504).

RESULTS

Trap yields varied considerably, with a maximum of 34 *Nautilus* in a single trap (including four *N. scrobiculatus*); the largest single yield of *N. scrobiculatus* (seven specimens, along with 10 *N. pompilius*) was obtained in a trap set overnight at a depth of *ca.* 200 m. However, the species is not common; the total yield for three trapping periods in 1984 (June–July, October–November) and 1985 (May–June) was 220 *N. pompilius* and 30 *N. scrobiculatus*. Many traps lacked the rarer species altogether. Off Ndrova Island, 12 traps set for one to four nights yielded a total of 180 specimens of *N. pompilius* and 29 specimens of *N. scrobiculatus*. At Komuli, traps set six times for one to 10 nights yielded only one specimen of *N. scrobiculatus* and 40 specimens of *N. pompilius*.

Our experience suggests that the distribution of *N. scrobiculatus* may prove to be spotty. It was not encountered at three other sites in the Papua New Guinea region (near Kavieng, Lae, and Port Moresby), where trapping for *N. pompilius* was successful (figure 1, and Saunders & Davis, 1985).

In addition to the descriptive account provided here, results of morphologic and genetic analyses of variation in the Papua New Guinea *Nautilus* will be reported by Swan and Saunders (in press) and Woodruff *et al.* (in press), and surveys of shell epizoans and predation will be presented by Landman *et al.* (in press) and Saunders *et al.* (in press).

Class **Cephalopoda** Cuvier, 1798
Subclass **Ectocochlia** Schwartz, 1894
Order **Nautiloidea** Hyatt *in* Zittel, 1900
Family **Nautilidae** de Blainville, 1825
Genus *Nautilus* Linnaeus, 1758

Nautilus scrobiculatus Lightfoot, 1786
(figures 1, 2, 4, 6–10; table 1)

Description

The shell of this species is generally *ca.* 180 mm diameter at maturity, and is readily distinguished by the large, vertical-walled umbilicus (*ca.* 20% shell diameter) that exposes the earlier whorls, back to the protoconch. The delicate, largely non-bifurcating brown to yellow-brown color bands are concentrated on the upper flanks of the shell, and coalesce across the venter. Relatively strong longitudinal (concentric) lirae intersect with growth lines, providing a strongly reticulate sculpture, reflected in the species name.

The 30 live-caught specimens from Manus include 25

Table 1. Shell dimensions (maximum diameter and aperture width measured beneath occular sinus) and total weight (shell plus body in air) of *Nautilus pompilius* and *N. scrobiculatus* from Manus, Papua New Guinea (arranged by sex). Note that all animals are mature.

	Shell diameter (mm)			Shell width (mm)			Total weight (g)		
Sex	Range	Mean	s.d.	Range	Mean	s.d.	Range	Mean	s.d.
Nautilus pompilius									
Females (n = 32)	142–173.8	157.2	8.8	61–81.8	70	4.9	450–820	590.8	94.8
Males (n = 97)	157–198.5	178.2	8.2	63.5–91.8	83	4.4	445–1,200	908	119.3
Total (n = 129)	142–198.5	172.9	12.4	61–91.8	79.8	7.2	445–1,200	830.6	177.2
Nautilus scrobiculatus									
Females (n = 4)	168.2–178.4	171.6	4.6	75.5–80.5	77.9	2.3	710–802	764.3	44.8
Males (n = 21)	173.5–196.8	181.3	5.4	78–95.2	84.7	4.3	770–1,340	938	137
Total (n = 25)	168.2–196.8	179.8	6.3	75.5–95.2	83.6	4.8	710–1,340	907.8	142

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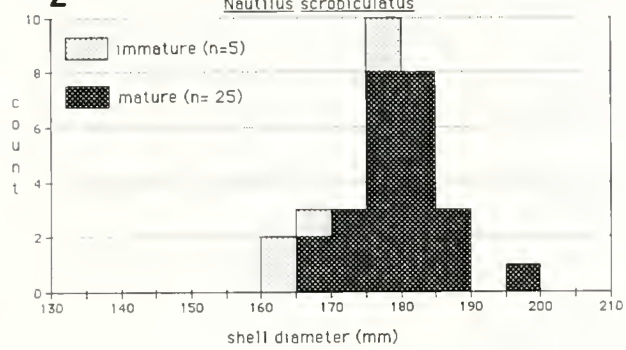

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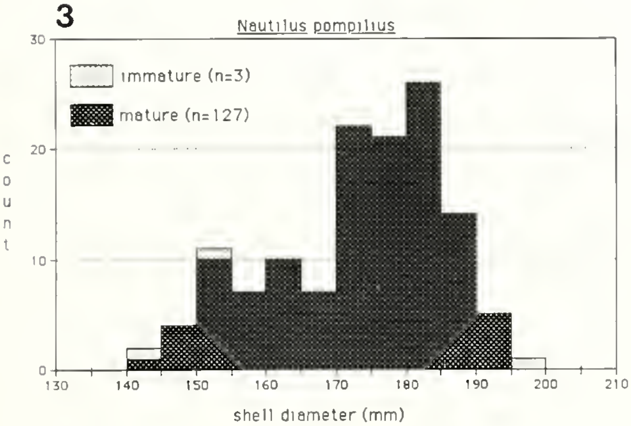

Figures 2, 3. Frequency distributions of live-caught specimens of *Nautilus scrobiculatus* and *N. pompilius*, showing size range (maximum shell diameter mm) and predominance of mature individuals (see table 1 for additional data).

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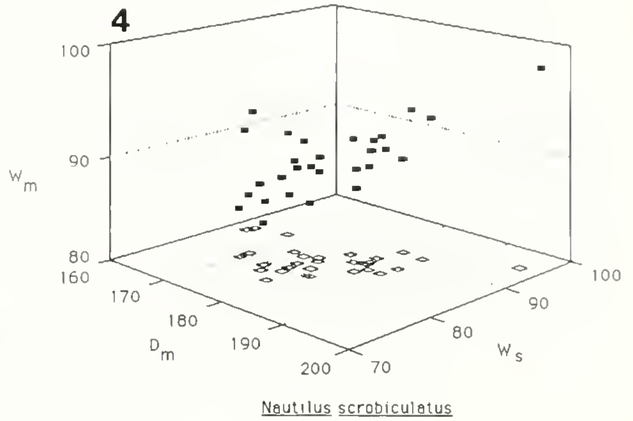

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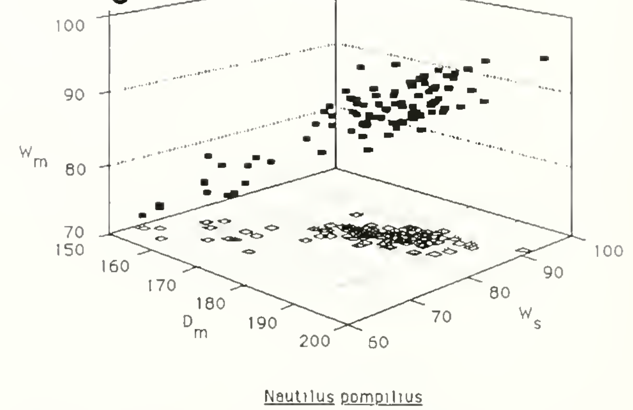
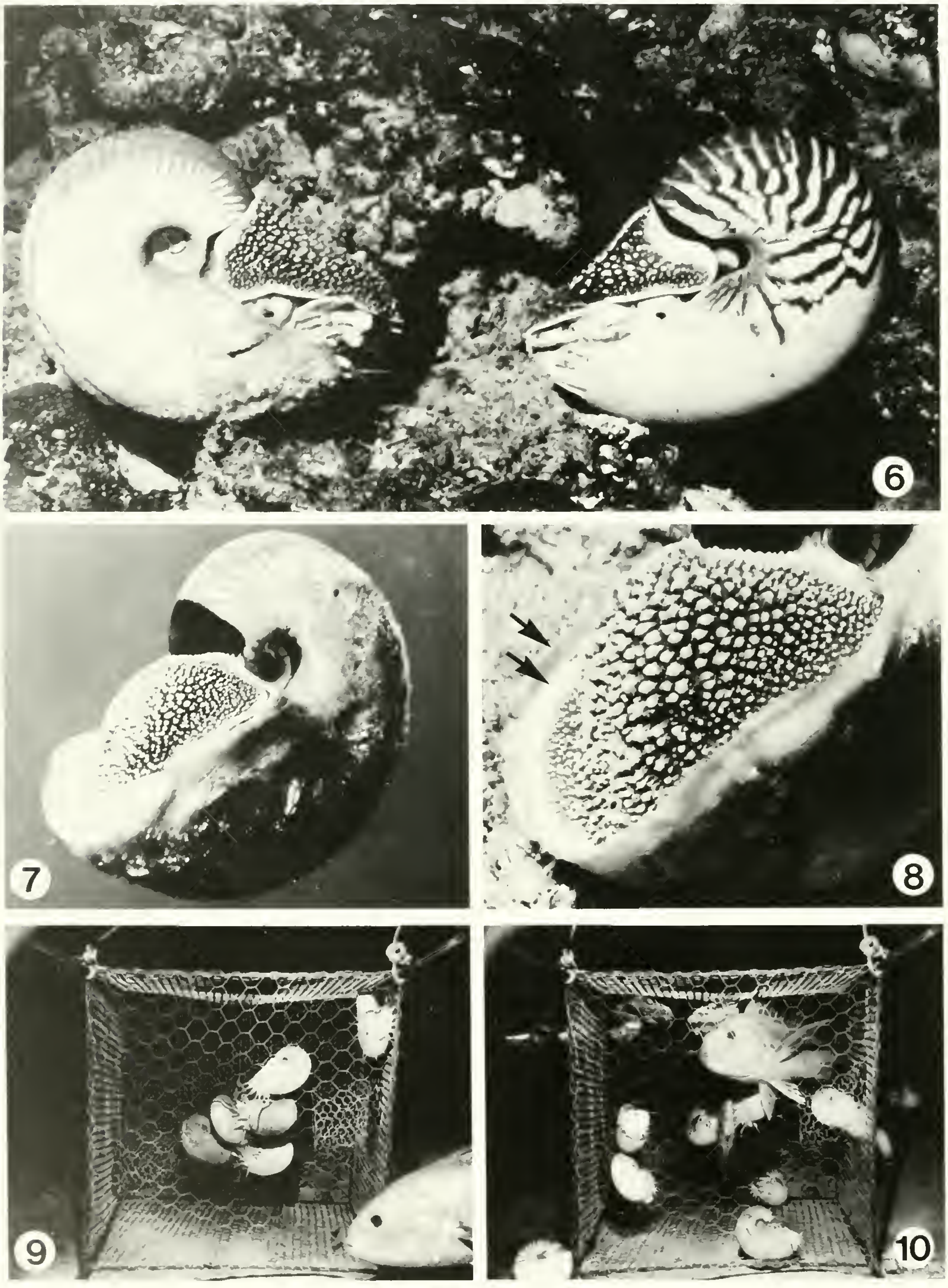


Figures 4, 5. Plots of maximum shell diameter (D_m), maximum shell width (W_m), and shell width beneath the ocular sinus (W_s) in *N. scrobiculatus* (n = 29) and *N. pompilius* (n = 124), on shadowed 3-D scattergrams. In *N. pompilius*, mature females are typically smaller (mean D_m 157 mm) and narrower (mean W_s 70 mm) than males (mean D_m 178 mm, W_s 83 mm); *N. scrobiculatus* shows less variation and less pronounced sexual dimorphism, but this may be an artifact of the smaller sample size.

fully mature animals ranging in size from 168.2 to 196.8 mm diameter (mean 179.8; figure 2, table 1). Total weight (shell plus body) ranges from 710 to 1,340 g (mean 907.8 g). Males outnumber females 4:1, a ratio characteristic of *Nautilus* populations in general (Saunders & Spinosa, 1978). Sexual dimorphism is present in *N. scrobiculatus* (table 1) but is not as pronounced as in other species (figures 4, 5, and see Saunders and Spinosa, 1978). Females (mean diameter 171.6 mm) are slightly smaller (5.3%) than males (mean 181.3 mm), they weigh 19% less (mean 764 *vs.* 938 g), and they have a narrower aperture, as measured below the ocular sinus (mean 77.9 mm in females, 84.7 mm in males); the latter reflects development of the spadix in mature males.

The periostracal layer: Perhaps the most striking and unexpected feature observed in *N. scrobiculatus* is the shaggy appearance presented by the living animal (figures 6, 7). This is due to a thick, golden, moss-like periostracum that covers all but the dorsal and umbilical portions of the shell in larger animals. In young animals the dorsal portion of the shell appears also to be covered, judging from deep-water remote photographs. The periostracal covering is composed of a series of interlayered semi-transparent sheets, or leaves, *ca.* 5–10 mm wide that extend the length of the aperture (figures 7, 8). This covering is relatively delicate and easily abraded, raising the question of how it survives the bump-scrape mode of travel along the bottom, which typifies *Nautilus* (Saunders, 1984). In other species of *Nautilus* (particularly in *N. belauensis* Saunders, 1981 from Palau), the periostracum may be fairly prominent in juvenile specimens, giving the shell's surface a somewhat slimy texture, but it is not present on the shells of mature animals (Saunders, 1983).

Details of the hood: The hood texture of this species is unique among the species of *Nautilus*. Willey (1902:744) commented on the flat-topped angular areas separated by deep grooves, as shown in his illustration (1902: pl.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78, fig. 3). The hood texture of none of the Manus specimens shows such a flattened pattern. Instead, it is covered with a series of white, conical bumps, ranging from *ca.* 1 to 5 mm diameter (figures 7, 8). The amount of relief varies from specimen to specimen, but it is not known whether individual animals can vary the texture. The difference between Willey's observations and those reported here may be due to the condition of his specimen, or it may represent geographic differentiation (Milne Bay is approximately 1,000 km southeast of Manus).

The only other difference noted in living *N. scrobiculatus* is a slight, brownish pigmentation of the surface of some of the tissues, including areas of exposed mantle near the peristome, and some of the funnel surface. No other differences in the soft parts of any of the species of *Nautilus* have been described, although detailed comparative anatomical comparisons remain to be undertaken.

Nautilus pompilius Linnaeus, 1758
(figures 1, 3, 5, 6, 9–12; table 1)

Description

Nautilus pompilius, the type species for the genus, is the most common and widespread species of *Nautilus*. This species has been documented elsewhere (*e.g.*, Saunders, 1981, in press) and will not be described in detail here. However, it seems appropriate to describe certain distinguishing characteristics of the Manus form, which cohabits the forereefs with *N. scrobiculatus*.

Morphological data are available for 132 live-caught specimens, including 92 specimens trapped off Ndrova, and 40 from nearby Komuli. Of these, 127 specimens were mature, and ranged in size from 142 to 198.5 mm diameter (mean 172.9 mm; figure 3, table 1), and total weight ranged from 445 to 1,200 g (mean 830.6 g). It is worth noting that the wide range in the latter parameter largely reflects variation in contents of the animal's highly distensible crop, which may be engorged with food weighing as much as 25% of the animal's body weight.

Females comprised 23.6% of the animals trapped off Manus. Sexual dimorphism is manifested in mature animals by differences in shell size, with females almost 12% smaller (mean 157.2 *vs.* 178.2 mm diameter), and 35% lighter (590.8 *vs.* 908 g total weight), and by differences in shell width [mean width measured below the ocular sinus (W_s) 70 mm in females, 83 mm in males; Table 1]. This dimorphism is noticeably greater than in *N. scrobiculatus* (figures 4, 5), but is similar to that observed in other populations of *N. pompilius* and in *N. belauensis* (Saunders & Spinosa, 1978; Saunders & Ward, in press).

Shell coloration: The pattern of shell coloration in the Manus specimens of *N. pompilius* differs somewhat from that observed elsewhere in the Papua New Guinea region, as well as from other more distant sites, including the Philippines and Fiji. The major difference is in the relatively greater amount of coloration of the shell. In the Manus specimens, the color bands tend to coalesce over the top of the shell, producing a solid, reddish brown dorsal surface. By contrast, *N. pompilius* coloration typically includes either relatively narrow stripes, or a reduced number of stripes, and the stripes extend across the periphery of the shell, separated by white bands. In a few of the Manus specimens, the umbilical region lacks coloration. This pattern of coloration is common in some of the southern Papua New Guinea populations, particularly in specimens from off Lae and Port Moresby. More detailed analysis of the shell coloration and morphology of this population will be provided by Swan and Saunders (in press).

Umbilication in *N. pompilius*: The shell of *Nautilus pompilius* has a small umbilicus (*ca.* 5% shell diameter), which is filled with a callus, beginning at about 75 mm diameter (after formation of the first two whorls) in typical Philippine examples. This deposit is apparently secreted by a portion of the mantle behind and just above the eye. Rarely, the callus may be lacking on either or on both sides of the shell.

An open umbilicus was observed in only one live-caught Manus specimen, but several drifted specimens showing an open umbilicus have been obtained. One of these (figures 11, 12), shows a uniquely enlarged umbilicus on one side of the shell; its appearance is so unusual that it initially aroused speculation that it might represent a *pompilius*/*scrobiculatus* hybrid. Recently, several additional shells of *N. pompilius* showing this feature have also been obtained from Indonesia and from the Philippines, and it seems sufficiently unique as to warrant description.

The Manus specimen is mature, probably a female, 157.5 mm in diameter, and the umbilicus measures approximately 15 mm diameter. Close examination shows that until *ca.* 50 mm shell diameter, the umbilical margin was forming normally and the umbilicus was just beginning to close, when a sudden change in the umbilical

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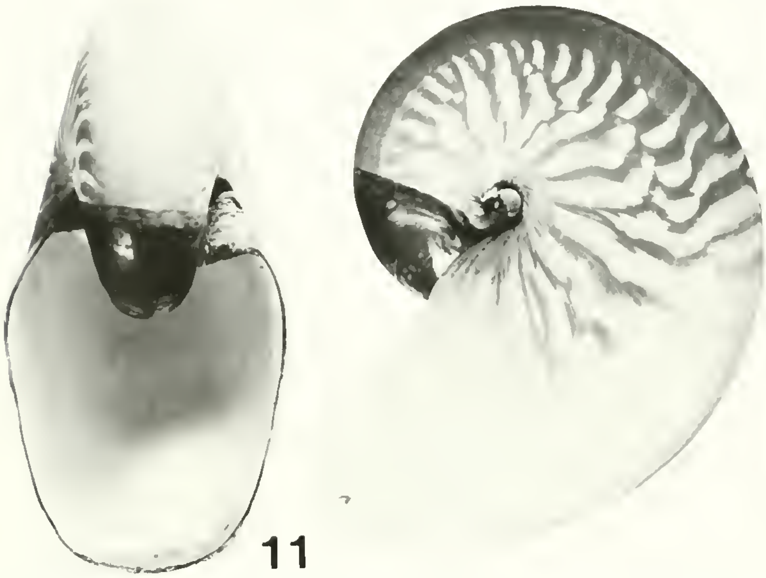
Figures 6–10. Underwater photographs of *Nautilus scrobiculatus* and *N. pompilius*, taken off Ndrova, Manus Province. **6.** *N. scrobiculatus* (on left) and *N. pompilius* photographed in shallow water, shortly after trapping at 270 m depth (×⅓). **7.** *N. scrobiculatus* in shallow water, showing heavy periostracal covering on shell, heavily textured hood, and distinctly umbilicate shell (×⅓). **8.** Closeup of previous speicmen, showing hood texture and details of periostracum (upper arrow points to last periostracal leaf, attached to shell margin, shown by lower arrow; ×½). **9, 10.** Deep-water remote camera photographs taken off Ndrova, 5-30/31-85, at 270 m depth, showing *N. scrobiculatus*, *N. pompilius*, and deep-water snapper (*Etelis carbunculus*) attracted to baited trap (entrances on each side; for details of techniques see Saunders, 1984; trap width *ca.* 1 m).



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Figures 11, 12. Apertural, lateral, and umbilical views of a drift shell of a mature female (?) *N. pompilius* from Manus (USNM 816702), showing an unusual, enlarged umbilicus on one side of the shell. The abnormality apparently began with sudden withdrawal of callus-secreting mantle at point shown by arrow; subsequently, umbilicus was enlarged The heavy black deposits on the umbilical wall indicate this is a pathologic feature, produced by disease or injury to the mantle, rather than representing hybridization between *N. pompilius* and *N. scrobiculatus* (11, ×½; 12, ×3).

shape occurred (figure 12). The pattern in the Indonesian specimen is remarkably similar, occurring just as the umbilicus was closing, although the umbilicus is proportionately smaller. In the Philippine shell, the umbilical enlargement begins later (*ca.* 100 mm diameter), after the umbilicus had closed.

DISCUSSION

Function of *Nautilus* periostracum: Functional explanations for heavy periostracum in mollusks are varied, but include protection against shell boring—by both endolithic borers and predators—and against encrustation by epizoans (Bottjer & Carter, 1980; Bottjer, 1981). *Nautilus* is known to be vulnerable to *Octopus* attacks, as shown by the number of drill holes observed in the shells of both live-caught and drifted shells (Saunders *et al.*, in press; see also Arnold, 1985: fig. 11a). Presumably, the slippery surface provided by the periostracum would make the shell difficult to grasp. Anti-fouling protection would also be advantageous, for *Nautilus* must overgrow its own earlier whorls. This would seem to be particularly critical during the early stages of growth, in which the periostracum is most prominent. *Nautilus* must maintain near-neutral buoyancy throughout life, and could not afford to host an extensive epifauna on its shell exterior.

If an anti-fouling interpretation for the shaggy periostracum of *N. scrobiculatus* is correct, it has not been entirely successful. A recent analysis of *Nautilus* epizoans by Landman *et al.* (in press), which included the specimens described here, showed that *N. scrobiculatus* had a much higher proportion of encrusted shells (92%) than *N. pompilius* (12–49%) or *N. belauensis* (68%). However, it was also noted that almost all of the epibiont encrustation in *N. scrobiculatus* occurred within the umbilicus—where the heavy periostracum is absent.

It may be relevant that *N. scrobiculatus* has the most strongly sculptured shell of any species of *Nautilus*. This may suggest that (a) roughly sculptured shell surfaces may benefit by extra periostraeal protection from epizoan settlement; or (b) it might also indicate that a thick periostracum requires a roughly textured surface for attachment.

It would be interesting to know the "cost" of the heavy periostraeal covering in terms of drag. SCUBA-based observations of *N. pompilius* and *N. scrobiculatus* in shallow water indicate that the latter species is not as strong a swimmer. It is also far less hardy than other species of *Nautilus*, in terms of its ability to withstand the rigors of trapping, being handled, etc.

Umbilication in *Nautilus*: Willey (1896) remarked on this feature, and went so far as to name a series of variants, based on degree of umbilical closure. Umbilication was also described by Mapes *et al.* (1979). However, lack of an umbilical callus in *N. pompilius* is regarded as a rare variation that does not warrant taxonomic designation. It has been reported in *N. pompilius* from the Philippines (in less than 0.025% of live caught specimens; Saunders, in press) and in *N. belauensis* only four of more than 1,100 trapped specimens lacked an umbilical callus (see Saunders, 1981: figs. 9, 10).

The sudden onset of umbilication, the fact that it is

accompanied by considerable black material (which is commonly associated with injury or stress), and the common presence of a normal umbilicus on the opposite side of the shell, all suggest that it is a product of trauma (either disease or injury) to the mantle in the umbilical region.

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LITERATURE CITED

Arnold, J. M. 1985. Shell growth, trauma, and repair as an indicator of life history for *Nautilus*. The Veliger 27:386–396.

Bottjer, D. J. 1981. Periostracum of the gastropod *Fusitron oregonensis*: natural inhibitor of boring and encrusting organisms. Bulletin of Marine Science 31:916–921.

Bottjer, D. J. and J. G. Carter. 1980. Functional and phylogenetic significance of projecting periostracal structures in the Bivalvia (Mollusca). Journal of Paleontology 54:200–216.

Knight, R. L. 1975. The chambered nautilus newsletter. Delaware Museum of Natural History, Greenville, DE.

Landman, N. H., W. B. Saunders, J. E. Winston, and P. J. Harries. In press. Incidence and kinds of epizoans on the shells of living *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

Lightfoot, J. 1786. A catalogue of the Portland Museum, lately the property of the Duchess Dowager of Portland, deceased: which will be sold by auction by Mr. Skinner and Co. on Monday 24th of April 1786 and the thirty-seven following days at twelve o'clock. London, 194 p.

Mapes, R. H., T. J. Frest, and S. M. Aronoff. 1979. Abnormal callus development in *Nautilus*. The Veliger 21:442–443.

Saunders, W. B. 1981. The species of living *Nautilus* and their distribution. The Veliger 24:8–17.

Saunders, W. B. 1983. Natural rates of growth and longevity of *Nautilus belauensis*. Paleobiology 9:280–288.

Saunders, W. B. 1984. The role and status of *Nautilus* in its natural habitat: evidence from deep-water remote camera photosequences. Paleobiology 10:469–486.

Saunders, W. B. In press. The species of *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

Saunders, W. B. and L. E. Davis. 1985. A preliminary report on *Nautilus* in Papua New Guinea. Science in New Guinea 11:60–69.

Saunders, W. B. and C. Spinosa. 1978. Sexual dimorphism in *Nautilus* from Palau. Paleobiology 4:349–358.

Saunders, W. B., C. Spinosa, and L. E. Davis. In press. Predation on *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

Saunders, W. B. and P. D. Ward. In press. Ecology, distribution, and population characteristics of *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

Stenzel, H. B. 1964. Living *Nautilus*. *In:* Moore, R. C. (ed.). Treatise on invertebrate paleontology. Part K. Mollusca 3. Geological Society of America and University of Kansas Press, Lawrence, p. K59–K93.

Swan, A. R. H. and W. B. Saunders. In press. Morphologic variation in *Nautilus* from Papua New Guinea. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

Willey, A. 1896. Zoological observations in the South Pacific. II. On the nepionic shell of the recent *Nautilus*. Quarterly Journal of Microscopical Science, New Series 39:219–231.

Willey, A. 1902. Contribution to the natural history of the pearly nautilus. Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere, collected during the years 1895, 1896 and 1897. Part 6. Cambridge University Press, Cambridge, England, p. 691–830.

Woodruff, D. S., M. P. Carpenter, W. B. Saunders, and P. D. Ward. In press. Genetic variation and phylogeny in *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London.

News and Notices

AMERICAN MALACOLOGICAL UNION 53RD ANNUAL MEETING

The annual meeting of the American Malacological Union will be held 19–23 July 1987 at Key West, Florida. In addition to contributed papers and poster presentations, symposia on Cenozoic molluscan communities of the Americas and biology of Polyplacophora will be convened. Other scheduled events include guided field trips to the marine and terrestrial molluscan communities of the tropical Florida Keys.

For more information on attendance and presentations, please address inquiries to:

William G. Lyons
President, AMU
4227 Porpoise Drive S.E.
St. Petersburg, FL 33705 USA
Telephone (813) 896-8626 or 895-6202

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The Conchologists of America Convention is scheduled for St. Louis, Missouri, from Tuesday June 23 to Saturday June 27, 1987. The Convention will be centered in the Days Inn at the Arch (formerly called the BelAir Hilton). There will be slide lectures by many well known conchologists and malacologists, a shell auction and the ever popular Bourse, comprised of shell dealers from around the world. Also available will be a ride on a paddle wheeler and a banquet.

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The sequence of sections should be: title page, abstract page, introduction, materials and methods, results, discussion, acknowledgements, literature cited, tables, figure captions, figures. The title page should include the title, author's name(s) and address(es). The abstract page should contain the title and abstract, which should summarize in 250 words or less the scope, main results and conclusions of the paper. The abstract may be followed by a maximum of 8 key words. All references cited in the text must appear in the literature cited section and vice versa. In the literature cited section, all authors must be fully identified and listed alphabetically. Follow a recent issue of THE NAUTILUS for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included in the pagination. Tables must be numbered and each placed on a separate sheet. A brief legend must accompany each table. Captions for each group of illustrations should be typed on a separate sheet and include a key to all lettered labeling appearing in that group of illustrations.

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Anatomy and Systematic Position of *Fastigiella carinata* Reeve (Cerithiidae: Prosobranchia)

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ABSTRACT

Fastigiella carinata is placed in the family Cerithiidae, close to the genus *Pseudovertagus* Vignal on the basis of conchological, radular, and anatomical characters. *Fastigiella* has a shell sculptured with three strong spiral cords, an aperture with a distinct anterior canal, a pseudumbilicus, missing in juveniles, and a siphonal fasciole. The operculum is ovate, corneous, and paucispiral with an eccentric nucleus, and the radula is taenioglossate. The animal has an unusual hypobranchial gland comprised of many transverse leaflets, a ridge dividing the anterior oviductal groove, and an open pallial oviduct with the seminal receptacle in the medial lamina of the posterior oviduct.

INTRODUCTION

The systematic relationship of *Fastigiella carinata* Reeve, 1848 to other prosobranchs has been uncertain and speculative since its description nearly 140 years ago. The genus has been thought to include only one living species and until now was known only from empty shells from the central Bahamas and northwestern Cuba. Even its familial relationships have been in doubt.

Fastigiella Reeve has been a puzzle to many workers. Reeve (1848) remarked in the original description that the shell is intermediate between *Turritella* Lamarck and *Cerithium* Bruguière, but he hinted that *Fastigiella* might be a *Buccinum*-like carnivore (*i.e.*, what would now be called a neogastropod). Reeve placed *Fastigiella* in the catch-all "family Canalifera" because of its characteristic anterior canal. Woodward (1851:129) placed it with a query after "*Nerinaea*" in the family "Cerithiadae" (= Cerithiidae *sensu lato*). H. Adams and A. Adams first placed *Fastigiella* in the Fasciolariidae (1853:155) but later in the Cerithiidae (1858:655). Chenu (1859:182) also assigned *Fastigiella* to the Fasciolariidae.

Most later malacologists have followed Woodward and H. Adams and A. Adams in placing *Fastigiella* near *Cerithium* in the Cerithiidae, albeit in some cases with doubts indicated. Concepts of the genus *Cerithium* and of the family Cerithiidae have been various and generally broad. Opinions on the relationships of *Fastigiella* within the superfamily Cerithiacea and related superfamilies (as presently conceived) have also been varied. For example, Mörch (1877:209), although placing *Fastigiella* near *Cerithium* (*sensu lato*), stated that *Fastigiella* is closest to a Recent "*Triphoris*" (= *Triphora* Blainville; Triphoridae) and to a Pliocene "*Cerithium*" (assigned by Wenz, 1940, to the Potamididae). More orthodox discussions and placements of *Fastigiella* are those of Fischer (1884:679), Tryon (1887:115,149), Thiele (1929:214), Pérez Farfante (1940:71), Wenz (1943:770), and Sarasúa and Espinosa (1977:2). Ford (1944:8) considered *Cerithidea* Swainson, 1840 (Potamididae) a subgenus of *Fastigiella*, which is incorrect nomenclaturally (*Cerithidea* having priority over *Fastigiella*). Moore (1971:1–2), on the basis of its rarity and the presence of a siphonal fasciole and prominent varices on the shell, suggested that *Fastigiella* is a neogastropod, probably belonging to the Fasciolariidae. Abbott (1974:105), while assigning *Fastigiella* to the Cerithiidae, wrote that "it may prove to be in a totally different family, possibly the Pyramidellidae."

Approximately 100 specimens are now found in museums and private collections. Hugh Cuming possessed the first known specimen as early as 1847, but recorded no locality data. Dr. C. M. Poulsen obtained an immature specimen from Eleuthera prior to 1877 (*F. poulseni* Mörch, 1877; herein regarded as a synonym). The American Museum of Natural History has a dateless specimen from a collection catalogued prior to 1900. The Rev. P. D. Ford collected several specimens in 1943 along the north coast of New Providence Island. From 1953 through 1986 several dozen specimens have been reported in the literature or have been collected by amateur conchologists. All collectors have found dead specimens from beach drift or in water less than 3 m in depth.

Recently, a living *Fastigiella* was collected by Joseph Lleida at New Providence Island, Bahamas, and preserved in alcohol. This specimen (USNM 859097), although not preserved well enough for histological study, was a mature female that provided an operculum, radula and preserved soft parts suitable for general anatomical study.

MATERIALS AND METHODS

The senior author studied the anatomy, radula, and operculum of a live-collected snail and also assembled some distribution records. Conchological studies, nomenclatural history, and geographic data are by the junior authors, Robert Robertson and R. Tucker Abbott.

The following abbreviations are used throughout the text: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; DMNH, Delaware Museum of Natural History; BM(NH), British Museum (Natural History); LACM, Los Angeles County Museum of Natural History; USNM, National Museum of Natural History, U.S. National Museum, Washington, DC.

Material examined: BAHAMAS: Nassau, New Providence Id. (LACM S1855); Brown's Point, Nassau, New Providence Id. (DMNH 65992, 65993; USNM 707161, 859097); Silver Cay and Hog Id., off Nassau, New Providence Id. (*fide* G. Fehling); Delaports Point, Clifton Pier, east end of Goulding Cay, New Providence Id. (D. Cosman, *leg.*); South West Reef, 7 mi south of New Providence Id. (D. Cosman, *leg.*); Cable Beach, New Providence Id.; Holms Cay, Berry Ids. (J. Cordy collection); mouth of Stafford Creek, east Andros Id. (DMNH 49248); off Small Hope Bay, east Andros Id. (DMNH 29236, 40987, Sue Abbott, *leg.*); Cowrie Reef, Andros Id. (DMNH 51344); Cave Cay, Exumas (D. Cosman, *leg.*); Guana Cay, Exumas (D. Cosman, leg.); Highburn Cay (J. Cordy, *leg.*); Sail Cay (G. Duffy, *leg.*); Wemys Bight, Eleuthera (AMNH); Millars, Eleuthera (M. McNeilus, *leg.*); Berry Islands, Eleuthera (*fide* R. Houbrick); Windemere Id., Eleuthera (AMNH); Governor's Harbour, Eleuthera (AMNH); Bottle Cay, Schooner Cays, Eleuthera (ANSP 189519); Powell's Point, Eleuthera (DMNH 51837); west coast of Cat Island (W. G. Lyons, *in litt.*). CUBA: Cárdenas (USNM 434792); off Havana (Jaume collection); Santa Fe, 8 km west of Marianao, Havana (I. Pérez Farfante, *leg.*); Comacho Beach, 4 mi west of Varadero, Matanzas (J. Finlay, *leg.*); (DMNH 105578); Varadero Beach, Matanzas (J. Finlay collection; Museo Poey, *fide* Jaume & Sarasúa, 1943; ANSP 316919); Camarioca Reef area, Matanzas (J. Finlay, *leg.*); Bahía de Matanzas (R. Burquete, *leg.*).

A live-collected, mature, female snail was collected May, 1986 by Joseph Lleida at Brown's Point, New Providence, Bahamas, where it was found living in shallow water. The specimen, which had a shell 32.1 mm long and 11 mm wide, was preserved in 70% EtOH. It was kindly given to one of us, R. Tucker Abbott, and sent to the senior author for anatomical studies. The soft parts were extracted by breaking the shell in a small vise. The animal was dissected under a binocular dissecting microscope. Shell pieces, apex, operculum, and radula were examined using a Zeiss Novascan-30 scanning electron microscope. This specimen and its parts (USNM 859097) are deposited in the National Museum of Natural History, Smithsonian Institution.

RESULTS

SYSTEMATIC DESCRIPTION

Family **Cerithiidae** Fleming, 1822
Subfamily **Cerithiinae** Fleming, 1822

Genus *Fastigiella* Reeve, 1848

Genus *Fastigiella* Reeve, 1848:14–15. Type-species: *Fastigiella carinata* Reeve, 1848, by monotypy.

Diagnosis: Shell large, turreted, high spired, sculptured with 3 major, strong, raised spiral cords per whorl, exclusive of body whorl. Aperture ovate, about ¼ the shell length, and with short, recurved anterior canal. Pseudumbilicus and siphonal fasciole present on mature adults. Taenioglossate radula with lateral teeth having large basal plate and long lateral extension; marginal teeth long, hook-like. Paired salivary glands in front of nerve ring. Hypobranchial gland comprised of many transverse leaflets. Strong longitudinal ridge bisects distal oviductal groove of pallial oviduct.

Remarks: Various fossil species have been referred to *Fastigiella* (*e.g.*, by Cossmann, 1906:93–95). The only one appearing to us as possibly belonging in the genus is "*Cerithium*" *rugosum* Lamarck, 1804, of the Middle Eocene of France. *Mellevillia* Cossmann, 1889, named as a Lower Eocene "section" of *Fastigiella* from France, has none of the characteristics of the genus. The Eocene fossil, *Zefallacia australis* (Suter, 1919) somewhat resembles *Fastigiella*.

Fastigiella is a monotypic genus restricted to a small area of the western Atlantic, *i.e.*, the central Bahamas and northwestern Cuba. Its closest relatives appear to be in the cerithiid genus *Pseudovertagus* Vignal, which is now confined to the Indo-Pacific. "*Fastigiella*" *squamulosa* Pease, 1868, from the Tuamotus (Polynesia), is a high-spired Recent *Coralliophila* species.

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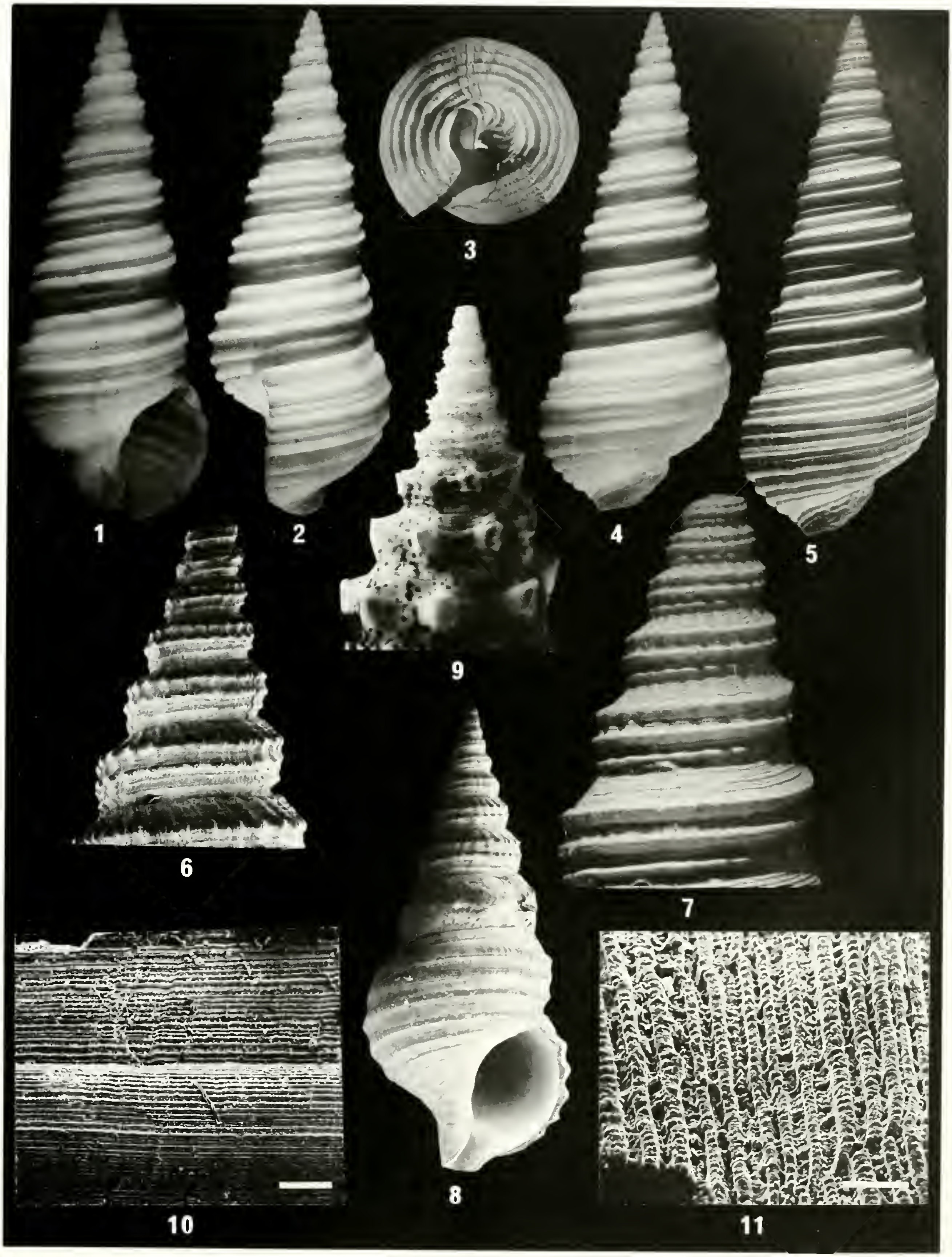
Figures 1–5. *Fastigiella carinata* Reeve from Holms Cay, Berry Islands, Bahamas. Note light tan spiral band adjacent to suture. Length 44.4 mm (J. Cordy collection). **1.** Apertural view showing anal fasciole and pseudumbilicus. **2.** Lateral view, showing configuration of outer lip. **3.** Basal view, showing reflected anterior canal and basal sculpture. **4.** Dorsal view. **5.** Dorsal view of shell whitened with ammonium chloride to enhance sculptural details. **Figures 6–8.** *Fastigiella carinata*, juvenile from Nassau, New Providence Id., Bahamas. Length 12 mm (J. Lleida collection). **6.** Scanning electron micrograph of early whorl sculpture of specimen in figure 8 (protoconch missing). **7.** Detail of midwhorl sculpture of shell in figure 8. **9.** Upper whorls of *Pseudovertagus aluco* Vignal, showing early sculpture similar to that of adult *Fastigiella*. Total shell length 79 mm. **Figures 10, 11.** Scanning electron micrographs showing microscopic spiral striae (fragments of USNM 859097). **10.** Scale bar = 200 μm. **11.** Close up of spiral striae showing microscopic cancellate sculpture of striae. Photograph turned 90 degrees; scale bar = 600 μm.



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Fastigiella carinata Reeve

Fastigiella carinata Reeve, 1848:15, 1 fig. Type-locality unknown; subsequently selected Eleuthera, Bahamas (Sarasúa and Espinosa, 1977:4); two syntypes: BM(NH) 1986272; 1860 122–123. Woodward, 1851:129; H. Adams and A. Adams, 1853:155,655, pl. 16, fig. 7; Chenu, 1859:182, fig. 916; Tryon, 1882:249, pl. 70, fig. 64; pl. 10, fig. 46; Thiele, 1929:214; Wenz, 1943:770, fig. 2230; Pilsbry, 1953:77–78, pl. 6, figs. 2, 3; Kline, 1953:142; Jensen, 1968:6–7, fig.; Abbott, 1974:105, fig. 1009; Sarasúa and Espinosa, 1977: 1–11, fig. 1; Abbott and Dance, 1982:68, fig. 6.

Fastigiella poulseni Mörch, 1877:207–208. (Type-locality: Eleuthera, Bahamas; holotype: an immature shell without a pseudumbilicus.) Poulsen, 1878:9, no. 533; Pérez Farfante, 1940:71, pl. 13, fig. 3; Jaume and Sarasúa, 1943:57.

Fastigiella (*Cerithidea*) *carinata* Reeve. Ford, 1945:8.

Description: *Shell description (figures 1–8, 10, 11):* Shell length 11.2–48.4 mm [mean 33.0 mm; n = 16; observed up to 53.2 mm in Cuba (Sarasúa & Espinosa, 1977:5, 11)]. Spire high; spire angle 25–35 degrees (mean 28 degrees). Shell fairly thin to thick, white, sometimes with brownish orange or light tan spiral band (figures 1, 2, 4). Periostracum inconspicuous, but scale-like when viewed microscopically (figures 10, 11). Protoconch unavailable (shell prone to decollation). Teleoconch whorls 11.7+. Teleoconch initially with a subsutural ramp and 3 spiral cords, the uppermost forming a slight shoulder (figures 6, 7). Upper whorl cords with slight nodes or prickles caused by weak, regularly spaced axial growth wrinkles. Lower whorls of large shells with increasing number of spiral cords (figures 1–5), the new ones beginning as intercalations. Subsutural ramp becoming a wide, slightly raised cord accompanied below by a smaller cord. All other cords larger and about equal-sized on large shells. Counting all 3 kinds of cords, there are 11–14 on last whorl of large shells. Fine spiral threads on all cords and interspaces (figure 10). Pair of subperipheral keels absent on small shells. Suture slightly impressed. Several irregularly spaced faint varices present on lower whorls of large shells (figure 3). A short, somewhat recurved but deeply incised anterior canal present (figures 1, 3, 8). On small shells its left edge is a slightly raised spiral fold joining the columella distally; on large shells a faint swelling in its place (figure 1). Anterior canal variable in width (averaging fairly wide) and, after shell attains length of about 25 mm, leaving a spiral siphonal fasciole with strong growth lines (figure 3). A pseudumbilicus (figure 1) of variable width (up to 1.3 mm) and morphology develops after shell reaches length of about 25–35 mm. Parietal callus thin, conforming with underlying cords on small shells; on large shells callus thick and not conforming, so that there can be 1–3 false umbilical chinks formed by cord interspaces to produce a siphonal fasciole. Faint, wide posterior canal present on large shells, viewed aperturally (figure 1). Columella roundly concave. Outer lip thin in juveniles and thick on large shells; no thick peritreme callus, eversion of outer lip, or upturned suture near outer lip.

External anatomy (figure 18): Adult female (shell 32 mm long) body slender, tapering, and comprising 6 or 7 whorls. Animal whitish with tiny red dots on head-foot. Head has conspicuously large, broad, spade-shaped snout, bilobed at the tip (figure 18, sn). Pair of stubby cephalic tentacles and tiny black eye at peduncular base of each tentacle (figure 18, t). Foot thick and muscular. Propodial mucus gland (figure 18, mg) is a deep slit along leading edge of anterior sole. Sole composed of thick, hard, yellowish tissue thrown into lumps. Large, dark brown, horny operculum (figure 17) thick, ovate, paucispiral with subcentral nucleus and filling the shell aperture. Columellar muscle (figure 18, cm) thick and short, about ½ mantle cavity length. Mantle edge thick and dorsally fringed with short papillae (figure 18, mp). Inhalant and exhalant siphons inconspicuous except for slight thickening of mantle edge. Posterior 5 whorls comprise digestive gland (figure 18, dg), which is overlain by ovary (figure 18, ov). The 2 whorls above body whorl accommodate the kidney (figure 18, k) and stomach (figure 18, st), respectively.

Mantle cavity: Mantle cavity deep and spacious, occupying about 2.5 whorls. Osphradium (figures 19, 20, os) a raised ridge, squarish in cross section, darkly pigmented and probably highly ciliated on each side. Osphradium begins about 2 mm behind distal end of ctenidium and extends for ⅔ ctenidial length. It lies closely adjacent to ctenidium, but deviates from it in region of inhalant siphon. Ctenidium (figures 19, 20, ct) a narrow, large, well-developed organ comprising long, triangular filaments with finger-like tips. Each filament has a supporting rod along its leading edge. Hypobranchial gland (figures 19, 20, hg) a highly developed, thick organ comprising a series of thin, transparent, semicircular leaflets that run adjacent to ctenidium and extend length of mantle cavity. Spaces between each leaflet filled with flocculent, acellular mucus-like material that may be secreted by epithelial lining of leaflets. Rectum (figures 19, 20, r) tubular and thick, filled with rod-shaped fecal pellets without sand and consisting of detritus.

Alimentary tract: Broad, spade-shaped snout (figure 18, sn) highly muscular and bearing relatively large buccal mass. Pair of small, semilunar, chitinous jaws comprising many small, overlapping scales at tip of buccal mass.

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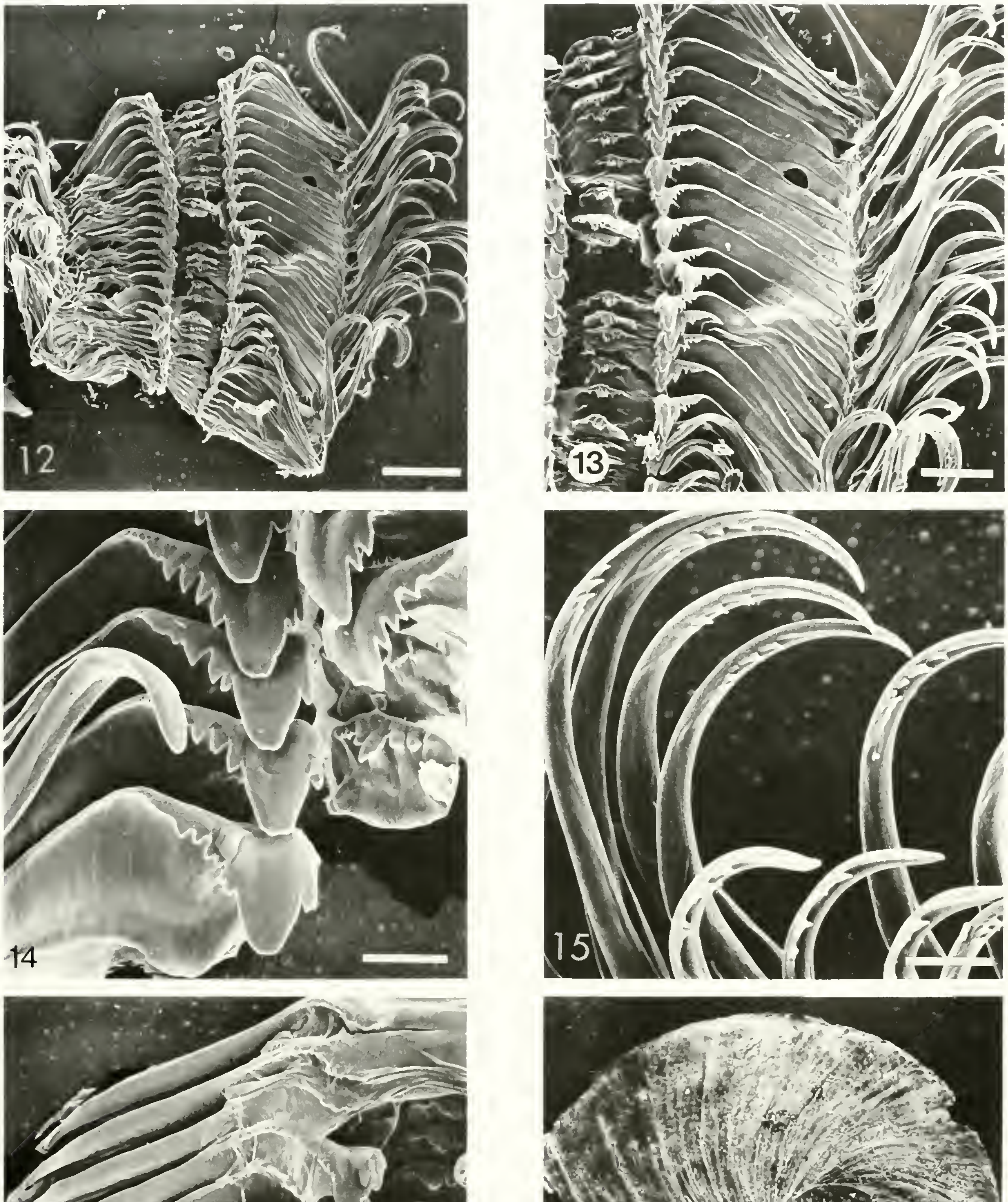
Figures 12–17. Scanning electron micrographs of radula and operculum of *Fastigiella carinata* (USNM 859097). **12.** View of part of radular ribbon with marginal teeth spread out. Scale bar = 125 μm. **13.** Half row of teeth showing long lateral tooth and narrow hooklike marginal teeth. Scale bar = 63 μm. **14.** Detail of rachidian tooth, showing basal plate and cusps of rachidian and lateral teeth. Scale bar = 25 μm. **15.** Tips of marginal teeth showing small denticles. Scale bar = 19 μm. **16.** Rachidian and lateral teeth showing long lateral-basal extensions of lateral teeth. Scale bar = 43 μm. **17.** Operculum. Length 8.4 mm.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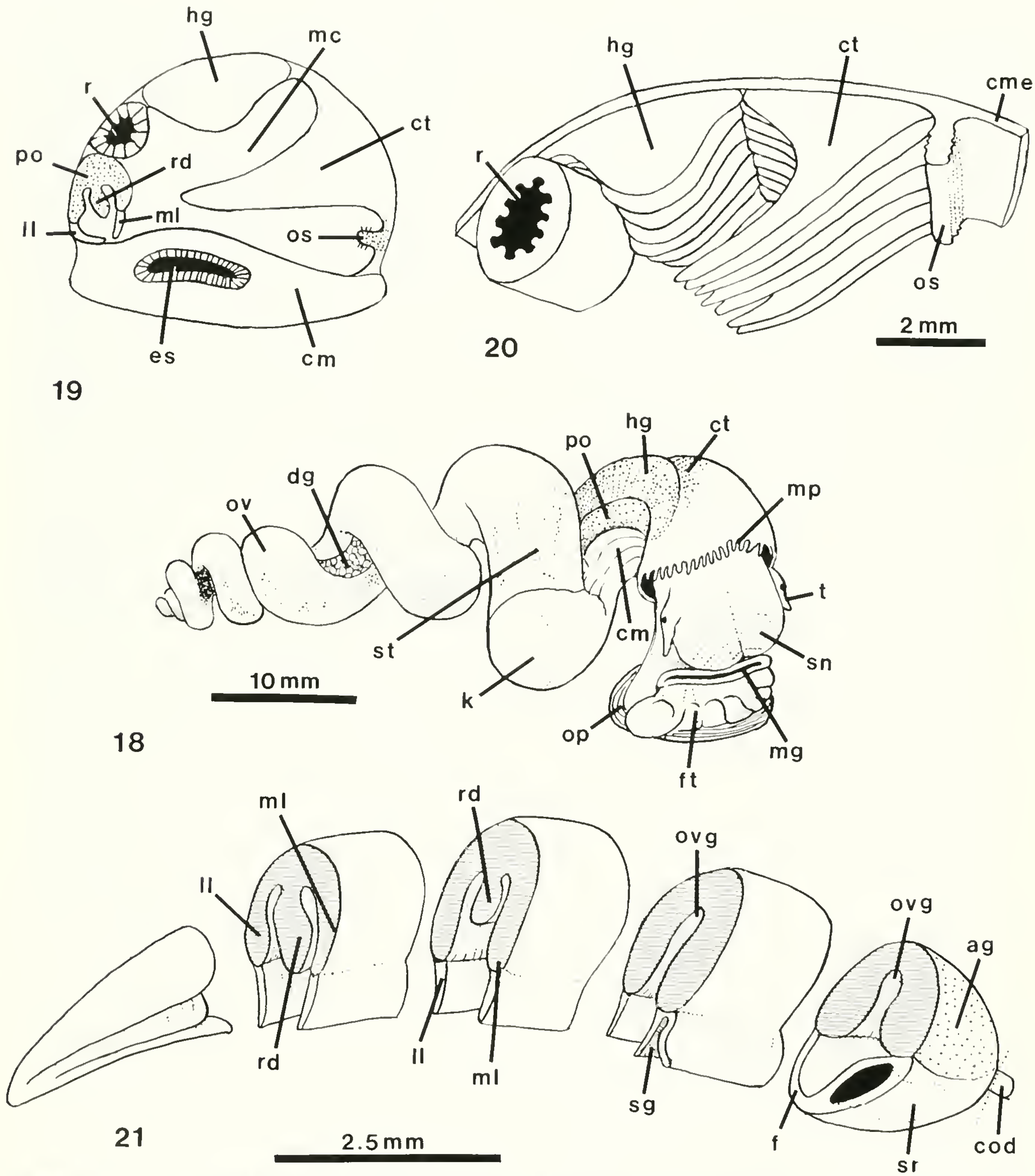

Figures 18–21. Anatomical features of *Fastigiella carinata*. **18.** External features of female viewed from the right. **19.** Schematic representation of cross section behind nerve ring showing morphological relationships of major mantle cavity organs. **20.** Schematic representation of section of mantle cavity organs exclusive of pallial gonoduct showing relationship of hypobranchial gland leaflets to rectum and ctenidium. **21.** Schematic representation of pallial oviduct and its internal components. ag = albumin gland. cm = columellar muscle; cme = cut mantle edge; cod = coelomic oviduct; ct = ctenidium; dg = digestive gland; es = esophagus; f = fusion of lateral and medial laminae; ft = foot; hg = hypobranchial gland, k = kidney; ll = lateral lamina; mc = mantle cavity; mg = mucus gland; ml = medial lamina; mp = mantle papillae; op = operculum; os = osphradium; ov = ovary; ovg = oviductal groove. po = pallial oviduct; r = rectum; rd = central ridge dividing anterior oviductal groove; sg = sperm gutter; sn = snout; sr = seminal receptacle; st = stomach, t = cephalic tentacle.

Buccal mass has long odontophore. Salivary glands consist of pair of weakly coiled tubes that originate in front of nerve ring and empty at dorsal anterior part of buccal mass near jaws. Salivary glands thicker anteriorly. Midesophagus slightly expanded and has large dorsal food channel. Large stomach occupies about 1.5 whorls and comprises short style sac, hyaline gastric shield, large central pad-like ridge, and enormous sorting area.

Radula (figures 12–16): Taenioglossate radula short, about $\frac{1}{16}$ shell length (L = 2.2 mm), and comprises around 280 tranverse rows of teeth. Rachidian tooth wider than high, with convex tip and squat, hourglass-shaped basal plate (figure 14). Cutting edge of rachidian tooth comprises central cusp flanked on each side by 3 smaller denticles. Lateral tooth conspicuously large with very long lateral extension of basal plate and weak central buttress that extends posteriorly (figure 16). Cutting edge of lateral tooth serrated with 2 or 3 inner denticles, a large, pointed central cusp, and 4–6 outer denticles (figure 14). The two marginal teeth (figures 13, 15) are narrow, elongate, curved hooks with pointed tips and are wider where attached to basal radular membrane. Outer marginal tooth slightly larger and less hooked than inner one. Marginal teeth serrated near their distal outer sides with 3–5 tiny, sharp denticles (figure 15).

Reproductive tract: Large, acinous ovary (figure 18, ov) overlies digestive gland and occupies the first 4 or 5 whorls. It appears to consist of large cells. Female pallial oviduct (figures 19, 21) a very long open tube, comprising lateral (figures 19, 21, ll) and medial (figures 19, 21, ml) laminae connected to mantle floor along their dorsal margins. Posterior end of pallial oviduct has thickened walls and is closed by fusion of the 2 laminae (figure 21, f). Thick albumen gland (figure 21, ag) at posterior end of pallial oviduct. Seminal receptacle (figure 21, sr) and sperm gutter (figure 21, sg) lie near posterior end of medial lamina. Oviductal groove (figure 21, ovg) formed at thick, glandular, connecting bases of these 2 laminae. Oviductal groove divided along its length by large, central ridge (figure 21, rd) that begins anteriorly and extends back a little past midpoint of pallial oviduct. Ridge tapers and ends just anterior to opening of sperm gutter to seminal receptacle on medial lamina. This ridge effectively divides anterior and median parts of the oviduct into 2 open chambers, 1 of which may function as spermatophore bursa. Male gonoduct unknown.

Nervous system: Nervous system epiathroid. Cerebral ganglia joined by short, but distinct, connective. Right pleural ganglion joined to right cerebral ganglion by short connective.

Distribution and Ecology

Distribution (figure 22): *Fastigiella carinata* is known only from the Great Bahama Bank and the northwestern coast of Cuba. The known distribution in Cuba is from Santa Fe, 8 km west of Marianao, Habana, west to Cardenas (Pérez Farfante, 1940:71, pl. 13, fig. 3; Sarasúa & Espinosa, 1977; USNM 434792), a coastline only about 140 km long that is not the nearest part of Cuba to the Bahamas. Although previously published Bahamian records were from Andros and Eleuthera only, *Fastigiella* has been found on the eastern coast of Andros Island; the northern coast of New Providence Island; the Berry Islands; the southwestern coast of Eleuthera and the nearby Schooner Cays; Cat Island; Exuma Cays. This species appears to be absent from the Little Bahama Bank.

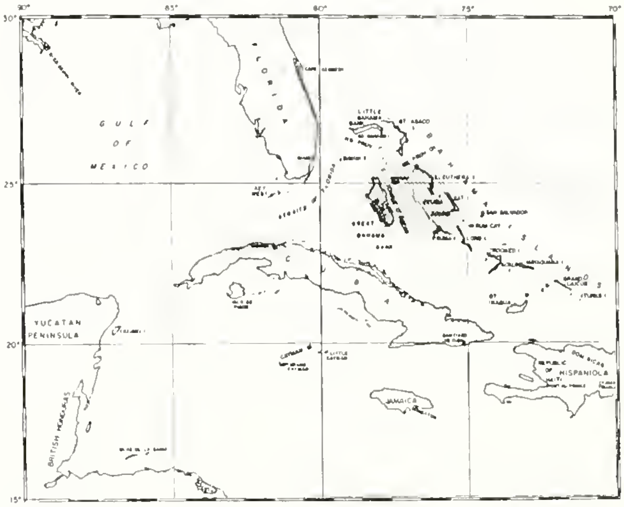

Figure 22. Geographical distribution of *Fastigiella carinata* based on available records, showing disjunct range.

Fastigiella carinata seems to be fairly rare in the localities discussed above, but may occur in other parts of the Bahamas and Cuba that are not as conchologically well known. Sarasúa and Espinosa (1977), who knew of 13 Cuban and only three Bahamian shells, stated that the species is more common in Cuba than in the Bahamas. We have been able to study many Bahamian and only 3 Cuban shells. Like such other shallow water species as *Cittarium pica* (Linnaeus) and *Turbinella angulata* (Lightfoot), this Bahamas-Cuba species has not been reported in Florida or Bermuda.

Ecology: Not much can be said about the ecology of *Fastigiella*. All of the shells available to us are slightly to moderately decollated (figures 6, 7), with not even part of a protoconch present. As the smallest intact whorl width is 0.7 mm, larval development could be planktotrophic or lecithotrophic. Although spawn and larvae remain unknown, the restricted geographic range suggests lecithotrophy or direct development.

The single, live-collected female described herein was found after a five-day blow, intertidally in a small hole on a rocky shelf bordering deeper sand and grass banks. As only one living specimen has been found, it is not certain that this is the normal habitat. Frequently, empty shells are inhabited by hermit crabs which also occur in other shallow water species such as *Tegula fasciata* (Born) and *Cerithium litteratum* (Born). The alimentary tract and fecal pellets indicate typical cerithiacean algal-detrital herbivory.

DISCUSSION

Shell variation: This species does not display the morphological variation that is so common among cerithiid genera such as *Cerithium*, *Clypeomorus* Jousseaume, and *Rhinoclavis* Swainson. Nevertheless, there are some variations that should be noted. Newly dead specimens may have a light tan spiral band adjacent to the suture (figures 1, 2, 4). Sarasúa and Espinosa (1977:6–7) recorded remnants of a brownish orange color pattern on some Cuban shells.

Differences between fully grown and immature shells are most pronounced in the columellar and siphonal areas of the body whorl. Immature shells (figure 8) lack the pseudumbilicus and siphonal fasciole that is present in fully grown specimens (figures 1–3). The narrow pseudumbilicus, which varies in width, and the siphonal fasciole develop after the shell reaches a length of 25–35 mm, as noted by Jensen (1967).

Several Cuban shells reach a length of 52–60 mm, while the largest Bahamian specimens observed are 45–48.4 mm. Fully mature specimens from Cuba, exceeding 35 mm in length and having a deep, narrow pseudumbilicus, differ in having six or seven evenly-sized spiral cords on the penultimate whorl, while those from the Bahamas have only three or four cords. We do not believe that this geographical difference is worthy of subspecific recognition. Cuming's specimen, illustrated by Reeve (1848:15) and copied by Woodward (1851), Tryon (1882), Wenz (1943), and others, is evidently a Bahamian specimen.

Comparative conchology: Before the live-collected specimen became available for study, one of us (Robertson) noted similarities between the shells of full-grown *Fastigiella* and young *Pseudovertagus* Vignal, a genus that has been monographed by Houbrick (1978:99–120). In the Recent fauna, *Pseudovertagus* is restricted to the tropical Indo-Pacific, where there are four species. Houbrick classified *Pseudovertagus* in the family Cerithiidae, subfamily Cerithiinae. Although full-grown shells of *Pseudovertagus* and *Fastigiella* are dissimilar, the sculpture of their upper whorls is very similar. The upper whorls of *Fastigiella carinata* (figures 6, 7) and *Pseudovertagus aluco* (Linné) (figure 9) are illustrated here. Both have three or four main spiral cords per whorl; the cords are prickly or noded; a subsutural ramp is faint to well-developed, and the whorls may or may not be slightly shouldered by one of the cords. *Pseudovertagus* and *Fastigiella* are the only living cerithiaceans known by us to have this apical sculpture. *Cerithium nodulosum* Bruguière, 1792, of the Indo-Pacific, is anomalous within its genus by having apical sculpture intermediate between that of *Cerithium sensu stricto* and those of *Pseudovertagus* and *Fastigiella*. This suggests that these three genera may be fairly closely related.

Pseudovertagus undergoes much greater ontogenetic sculptural change than *Fastigiella*. *Fastigiella* may be a neotenous relative to *Pseudovertagus*. Adults of the two genera both lack a prominent fold on the middle of the columella such as is present in species of *Rhinoclavis*, an Indo-Pacific genus close to *Pseudovertagus* (see Houbrick, 1978). The outer lip (viewed laterally) is not sinuous in either *Fastigiella* (figure 2) or *Pseudovertagus*, as it is in *Clavocerithium* Cossmann, another genus close to *Pseudovertagus* (see Houbrick, 1978). *Pseudovertagus* is not congeneric with *Fastigiella* as there are a number of conchological and anatomical autapomorphies distinguishing the latter taxon (see "Conclusion").

There are a few vague resemblances between *Fastigiella* and *Campanile* Fischer (Cerithiacea: Campanilidae), of which one relict species occurs in southwest Australia (Houbrick, 1981a). There are two Eocene species of *Pseudovertagus* in France, and two Miocene and Pliocene species in Florida (Houbrick, 1978:116–120), close to *Fastigiella*'s range.

Comparative anatomy: Study of the radula and anatomy has done much to clarify the systematic position of *Fastigiella*. Although only a single, poorly preserved specimen was studied, it was a sexually mature female and provided most of the important characters essential for comparison with other cerithiacean taxa.

Externally, the snail removed from its shell looks very much like some members of the Cerithiidae, such as *Cerithium*, *Rhinoclavis*, and *Pseudovertagus*. Notable features are the broad, bilobed snout, small cephalic tentacles, and tiny eyes (figure 18). The broad snout, contracted by preservation, is probably long and extensible in a living snail. In its contracted state it resembles those observed in *Diastoma* (Houbrick, 1981b:603, fig. 2) and *Campanile* Deshayes (Houbrick, 1981a:269, fig. 3, a, b), some *Cerithium* species, and especially *Pseudovertagus*. The mantle edge, fringed with small papillae (figure 18, mp), and the large, thick operculum (figure 17) are typical of those observed in cerithiids. The sole of the foot, particularly the anterior portion, was composed of thick, yellowish, hard tissue. This may be an unusual feature of *Fastigiella* foot morphology but is more likely an artifact of preservation. Many cerithiaceans have a ciliated groove or ovipositor on the right side of the foot, but no trace of these structures was seen in *Fastigiella*.

The mantle cavity is quite deep and typically cerithiacean in organization. The osphradium appears to be a raised ridge with wrinkled sides. It does not resemble the osphradium of cerithiid species of comparable size, but is more like those seen in potamidids, modulids, and thiarids. An important character is the unusual hypobranchial gland, which comprises a long row of transverse, thin, transparent leaflets and resembles a secondary ctenidium (figure 20, hg). Between the leaflets is thick mucus-like, flocculent, granular material. Due to the poor preservation of the animal, it was not determined if this material was formed by a breakdown of the epithelial lining of the leaflets or was merely hypobranchial gland secretion. The hypobranchial gland is unlike those of all other known cerithiaceans except *Pseudovertagus* species (family Cerithiidae), which have a nearly identical hypobranchial gland (Houbrick, personal observation). The hypobranchial gland of *Cerithium nodulosum* has prom-

inent raised transverse ridges and may be a transitional stage before the development of leaflets as found in *Fastigiella* and *Pseudovertagus* (Houbrick, personal observation). The hypobranchial gland of *Campanile* also has leaflets, but they are tiny and comprise many parallel rows (Houbrick, 1981a:274, fig. 4, A, hg). This gland is thus a much different structure in *Campanile* and its leaflet structure is not considered homologous with that seen in *Fastigiella*.

The pallial oviduct is a typically cerithiacean open duct. There is no spermatophore bursa, but its function may be taken over by the large closed portion of the posterior pallial oviduct. A spermatophore bursa in the outer or inner laminae of the pallial oviduct is a common feature in most cerithiids and its absence in *Fastigiella* is noteworthy. This pallial oviduct is very similar to those described for many cerithiids, potamidids, and *Diastoma* (see Houbrick, 1974, 1978, 1981b). The posterior end of the pallial oviduct is closed by fusion of the edges of the two laminae (figure 21, f). The pallial oviduct of *Fastigiella* differs from all other known cerithiacean pallial oviducts in having a large, swollen central ridge (figure 21, rd) at the base of the anterior oviductal groove. This ridge diminishes in size and disappears about midway along the pallial oviduct effectively forming two anterior oviductal grooves that merge past the middle of the pallial oviduct to form the main posterior oviductal groove. The function of this apomorphic structure is unknown. The ovary is large and differs from other observed cerithiid ovaries in being highly acinous. Males remain unknown but, on the basis of female anatomy, are expected to be aphallate and have open pallial gonoducts.

The alimentary tract is indicative of a microphagous, herbivorous mesogastropod. The short radula is different from that of most cerithiids in having long lateral teeth with conspicuous platelike lateral extensions (figure 16) and long hooklike marginals with microscopic serrations near their tips (figure 15). Similar lateral and marginal teeth occur in the cerithiids *Clavocerithium taeniatum* (Quoy & Gaimard) and *Rhinoclavis sordidula* (Gould) (Houbrick, 1975:101, figs. 9–12; 1978:71, pl. 40). Some planaxid radulae have similar lateral teeth (Houbrick, 1987). Although the salivary glands, or at least the left salivary gland, pass through the nerve ring in most cerithiids, the salivary glands of *Fastigiella* originate in front of the nerve ring. The esophagus widens behind the nerve ring, but there is no trace of an esophageal gland. A large dorsal food groove is present. The large, complex stomach with its extensive sorting area and large, raised central ridge (pad) is not unlike stomachs described for many other cerithiacean taxa. The number of openings to the digestive gland was not ascertained.

CONCLUSIONS

On the basis of the presence of a taenioglossate radula, proboscis structure and alimentary tract anatomy, we can confidently state that *Fastigiella* is a mesogastropod (order Caenogastropoda Cox, 1959). The open pallial oviduct and internal arrangement of the seminal receptacle and spermatophore bursa in the medial lamina strongly support an assignment to the superfamily Cerithiacea. Other external anatomical structures such as the head and snout, fringed mantle edge, corneous, ovate, paucispiral operculum, and propodial mucus gland are characters common in many cerithiacean families. Internal anatomical structures of the alimentary tract are likewise consistent with the cerithiacean anatomical organization.

Most characters, including those of the shell, indicate the family Cerithiidae as a suitable assignment for *Fastigiella*. Ontogenetic shell characters and a few anatomical characters suggest a close relationship to the genus *Pseudovertagus* Vignal, 1904. The unusual shell sculpture of three or four main spiral cords per whorl on the post-nuclear and upper whorls of *Fastigiella* is very similar to that seen in *Pseudovertagus* species. The broad snout is a character shared with *Pseudovertagus*. The hypobranchial gland comprised of transverse leaflets is likewise a synapomorphous character found only in *Pseudovertagus* and *Fastigiella*.

The pseudumbilicus and siphonal fasciole with one to three false umbilical chinks formed by cord interspaces in large shells are autapomorphic characters clearly defining *Fastigiella*. Other shell characters identifying the axon are the strong spiral sculpture of three or four rounded cords per whorl, and the short, slightly reflected siphonal canal.

The unusual, large ridge bisecting the anterior oviductal groove of the pallial oviduct is an autapomorphy that sets *Fastigiella* aside as a good genus. Other nonapomorphic anatomical characters including placement and origin of the salivary glands anterior to the nerve ring, the shape of the lateral and marginal teeth, and the unusual leaflets of the hypobranchial gland, are more equivocal, but together provide a distinctive set of characters defining this taxon as a separate genus.

No radular or anatomical characters have emerged from this study to suggest that *Fastigiella* should be given a higher than generic status. *Fastigiella* is a relictual, and geographically disjunct genus (at least on the basis of available material). We assign this genus in the Cerithiidae, close to the genus *Pseudovertagus*. Although it is unlikely that this assignment is incorrect, further study of males, other females, eggs, and larvae may provide more characters supportive of this classification. The systematic position advocated herein is based on knowledge of a single female snail and is tentative until more is known about this rare animal.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. New York, 663 p., 24 pls.

Abbott, R. T. and P. Dance. 1982. Compendium of seashells. New York, 411 p., illus.

Adams, H. and A. Adams. 1853–58. The genera of Recent Mollusca, 3 vols. London, 389 p., 138 pls.

Chenu, J. C. 1859. Manuel de conchyliologie et de paléontologie, Vol. 1. Paris, 508 p., 3707 figs.

Cossmann, M. 1906. Éssais de paléoconchologie comparée, Vol. 7. Paris, 261 p., 14 pls.

Cox, L. R. 1960. Thoughts on the classification of the Gastropoda. Proceedings of the Malacological Society of London 33(6):239–261.

Fischer, P. 1880–87. Manuel de conchyliologie et de paléontologie conchyliologique. Paris, 1369 p., 23 pls., 1158 figs.

Ford, P. D. 1944. A complete list of Bahamian shells collected and classified by the Bahamas Conchological Society. Privately published, Nassau, Bahamas, 11 p.

Houbrick, R. S. 1974. The genus *Cerithium* in the western Atlantic. Johnsonia 5(50):33–84.

Houbrick, R. S. 1975. *Clavocerithium* (*Indocerithium*) *taeniatum*, a little-known and unusual cerithiid from New Guinea. The Nautilus 89(4):99–105.

Houbrick, R. S. 1978. The family Cerithiidae in the Indo-Pacific. Part 1: the genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*. Monographs of Marine Mollusca No. 1:130 p., 98 pls.

Houbrick, R. S. 1981a. Anatomy, biology and systematics of *Campanile symbolicum* with reference to adaptive radiation of the Cerithiacea (Gastropoda: Prosobranchia). Malacologia 21(1–2):263–289.

Houbrick, R. S. 1981b. Anatomy of *Diastoma melanioides* (Reeve, 1849) with remarks on the systematic position of the family Diastomatidae (Prosobranchia: Gastropoda). Proceedings of the Biological Society of Washington 94(2): 598–621.

Houbrick, R. S. 1987. Anatomy, biology and phylogeny of the Planaxidae (Cerithiacea: Prosobranchia). Smithsonian Contributions to Zoology No. 445:57 p., 27 figs., 6 tables.

Jaume, M. L. and H. Sarasúa. 1943. Notas sobre moluscos marinos Cubanos. Revista de la Sociedad Malacologica "Carlos de la Torre" 1(2):52–61.

Jensen, D. 1967. *Fastigiella carinata*, a little known species. New York Shell Club Notes 128:6–7, 1 fig.

Kline, G. F. 1953. Another specimen of *Fastigiella carinata* Reeve. The Nautilus 66(3):142.

Lamarck, J. B. 1804. Suite des memoires sur les fossiles des environs de Paris. Annales du Muséum National d'Histoire Naturelle (Paris) 3:436–441.

Moore, D. R. 1971. What is *Fastigiella carinata*? Mollusk Chaser, South Florida Shell Club 9(8):1–2.

Mörch, O. A. L. 1877. Description d'une nouvelle espècie du genre *Fastigiella* Reeve. Journal de Conchyliologie 25:207.

Pérez Farfante, I. 1940. Adiciones a la liste de moluscos Cubanos. Memorias de la Sociedad Cubana de la Historia Naturalia 14(1):69–73.

Pilsbry, H. A. 1953. *Fastigiella carinata* Reeve, a little-known mollusk. The Nautilus 66(3):77–78.

Poulsen, C. M. 1878. Catalogue of west India shells. Copenhagen, 16 p.

Reeve, L. A. 1848. On *Fastigiella*, a new genus of shells of the Lamarkian family Canalifera. Proceedings of the Zoological Society of London 16:14–15.

Reeve, L. A. 1860. Elements of conchology, Vol. 1. London, 260 p., 21 pls.

Sarasúa, H. and J. Espinosa. 1977. Notas sobre el genero Antilliano *Fastigiella* (Mollusca: Mesogastropoda). Poeyana 171:1–11.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde. Band 1, Teil 1. Gustav Fischer, Jena, 376 p., 470 figs.

Tryon, G. W. 1882. Manual of conchology, first series, Vol. 4. Philadelphia, p. 5–276, 58 pls.

Wenz, W. 1940. Gastropoda, 1. Handbuch der Paläozoologie, Band 4. Part 4:721–960, text figs. 2085–2787; 1943, Band 6, Part 1.770 p., text figs. 3417–4211. Borntrager, Berlin.

Woodward, S. P. 1851. A manual of the Mollusca or a treatise of Recent and fossil shells. London, 338 p., figs., pls.

Note added in proof

Another live specimen of *Fastigiella* was recently collected by Kevan Sunderland in 1m depth on a patch reef, half buried on sand, at Marsh Harbour, Abaco, Bahamas.

Cataegis, New Genus of Three New Species from the Continental Slope (Trochidae: Cataeginae New Subfamily)

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ABSTRACT

Cataegis new genus, type species *C. toreuta* new species, is proposed to include three new species from continental slope depths (200–2,000 m): the type species and *C. meroglypta* from the Gulf of Mexico to Colombia, and *C. celebesensis* from Makassar Strait, Indonesia. Important shell characters are the prominent spiral cords, non-umbilicate base, and oblique aperture. The radula is unique among the Trochidae in lacking the rachidian, having the first pair of laterals fused and uncusped, and the first marginals enlarged. The gill is the advanced trochid type with well-developed afferent membrane. These characters do not correspond to an available subfamily; the new subfamily Cataeginae is therefore proposed.

INTRODUCTION

The two hitherto unknown species of trochids described here from continental slope depths in the Caribbean Sea and Gulf of Mexico were first examined by Quinn, who noted that shell characters of the two species are unlike those of any known genus of Trochidae. Epipodial and radular characters were later examined by McLean, who found a unique combination of radular features in one of the two species. A third member of the genus from slope depths in Indonesian waters was subsequently recognized by McLean in unidentified material received on loan from the Paris Museum. An unsuccessful search for a genus for these species prompted the present description of a new genus.

Although higher classification of Trochidae has been unsettled (Marshall, 1979), consideration of gill characters has led to new understanding (McLean, 1982), and a full review of higher classification of Trochacea is nearing completion by Hickman and McLean (in preparation). Full discussion of trochacean classification is deferred to that review. The new genus cannot be assigned to an existing trochid subfamily, necessitating the proposal of a new subfamily.

Institutional abbreviations used here are: ANSP (Academy of Natural Sciences, Philadelphia); FSBC I (Florida Department of Natural Resources, Bureau of Marine Research, St. Petersburg); FSM (Florida State Museum, University of Florida, Gainesville); LACM (Los Angeles County Museum of Natural History, Los Angeles); MCZ (Museum of Comparative Zoology, Harvard University, Cambridge); MNHN (Museum National d'Histoire Naturelle, Paris); TAMU (Invertebrate Collection, Texas A&M University, College Station); UMML (Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Coral Gables); USNM (U.S. National Museum of Natural History, Washington).

SYSTEMATICS

Family **Trochidae**
Cataeginae new subfamily

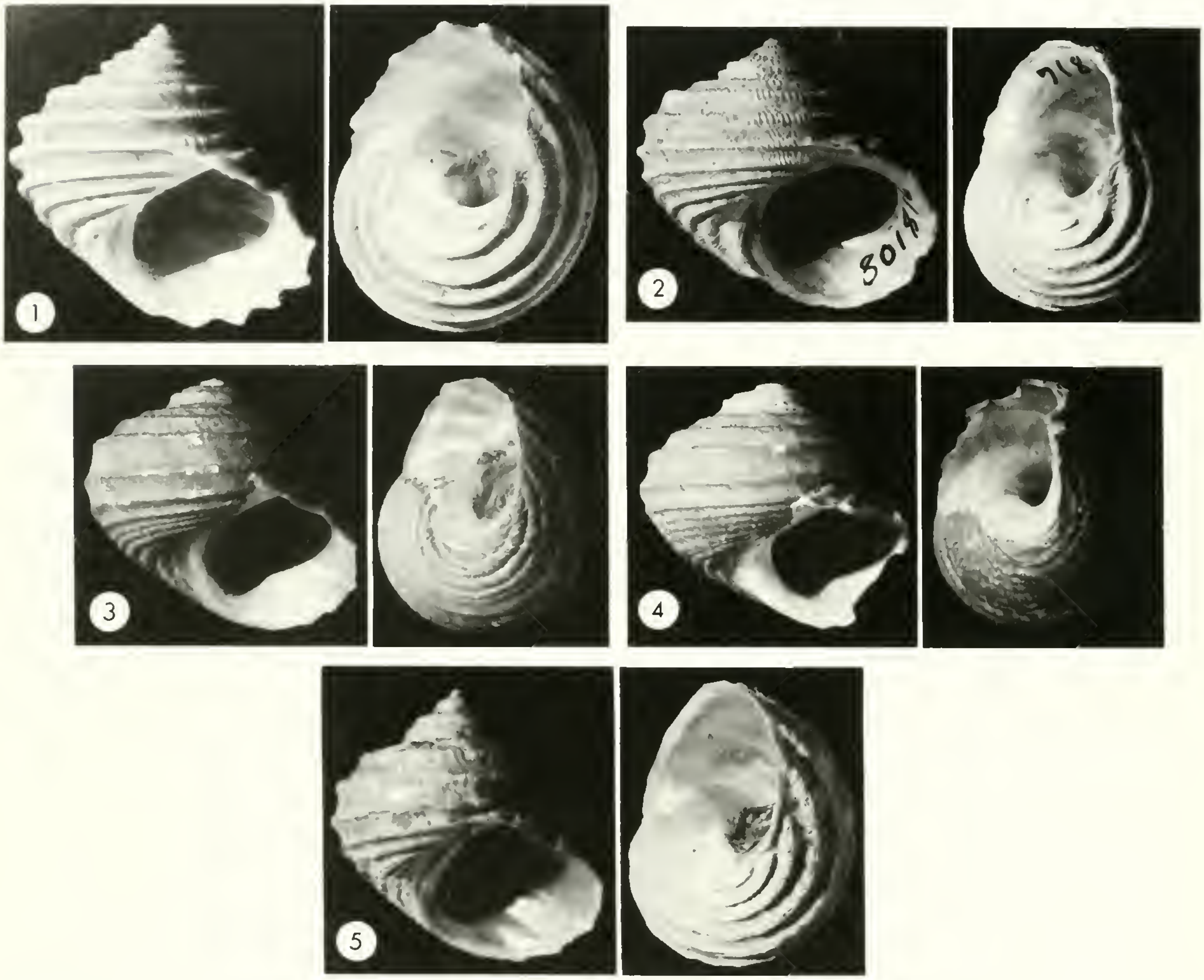
Type genus: *Cataegis* new genus.

Diagnosis: Shell non-umbilicate, with strong spiral cords, nacreous interior, oblique aperture, non-plicate columella, multispiral operculum.

Left gill bipectinate with long afferent membrane posterior to free tip. Snout expanded at tip; cephalic tentacles with broad bases, eyes on short peduncles; cephalic lappets lacking; epipodial tentacles small; left and right neck lobes well developed, finely fringed at edges; left neck lobe folded over, evidently capable of rolling to form incurrent siphon.

Radula lacking rachidian; lateral teeth 4 pairs, inner laterals fused, uncusped; second, third, and fourth laterals with simple, tapered, overhanging tips, shafts elongate with narrow frontal elements and large, triangular rear elements; inner edge of rear element interlocking with corresponding depression on outer edge of adjacent lateral tooth; latero-marginal plate not evident; marginals numerous, first marginal enlarged, second and third marginals decreasing in size, remaining marginals with sickle-shaped tips and up to 6 blunt denticles on each side of tip.

Discussion: Although shell characters are of minor importance in suprageneric classification of trochids, the combination of shell characters (strong spiral cords, lack

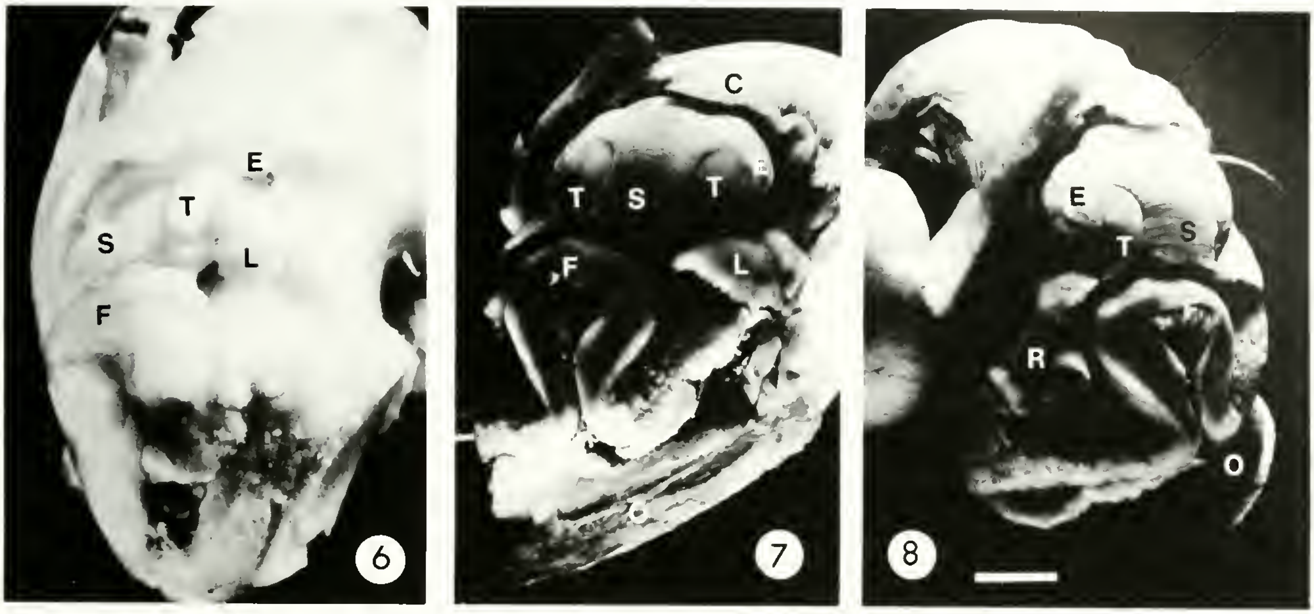


Figures 1–5. Shells of new species of *Cataegis*, apertural and basal views. **1, 2.** *Cataegis toreuta* new species. **1.** Holotype, off Colombia, USNM 784755, height 21.8 mm. **2.** Paratype, off Biloxi, Mississippi, USNM 801816, height 19.3 mm. **3, 4.** *Cataegis meroglypta* new species. **3.** Holotype, off Mississippi River Delta, Louisiana, MNHN uncat., height 17.8 mm. **4.** Paratype, off Colombia, USNM 784757, height 16.9 mm. **5.** *Cataegis celebesensis* new species. Holotype, MNHN uncat., Makassar Strait, Celebes, Indonesia, height 20.4 mm

of columellar plications, oblique, broadly expanding aperture) in *Cataegis* is unique.

Epipodial characters are those of generalized trochids in having well-developed left and right neck lobes, although most trochids have cephalic lappets and better-developed epipodial tentacles. Most deeper water trochid genera are included within the broadly defined subfamily Margaritinae (as used by Keen *in* Moore, 1960); these genera have in common a thin shell and most lack columellar plications. On shell and external anatomical characters it seemed likely that *Cataegis* should be related to such margaritine genera as *Cidarina* Dall, 1909. McLean (1982) noted, however, that genera of the old group "Margaritinae" have a primitive gill structure in which the afferent membrane is short. Contrary to all expectations for a deep-water genus, the gill structure of *Cataegis* is advanced, with a long afferent membrane like that of genera of the subfamilies Monodontinae, Trochinae, Calliostomatinae, and Solariellinae (as used by Keen *in* Moore, 1960).

The new subfamilial classification of Trochidae to be introduced by Hickman and McLean (in preparation) is, in large part, based upon a discrete radular plan for each subfamily. The radula of *Cataegis* fits nowhere within this scheme but represents yet another unique plan. Although there are genera in which the rachidian is uncusped, no other trochid group completely lacks the rachidian tooth and no other group exhibits a fusion of the bases of the first pair of lateral teeth, forming a "central element" that replaces the rachidian. The interlocking of the laterals is also unique; other radular plans show interlocking of the lateral teeth in different ways (for



Figures 6–8. External anatomy of *Cataegis*, photographs of retracted bodies. **6.** *Cataegis toreuta* new species (sta. P-388). **7, 8.** *Cataegis meroglypta* new species (holotype). Bar = 2 mm.
C, ctenidium; E, eye; F, foot; L, left neck lobe; O, operculum; R, right neck lobe; S, snout; T, cephalic tentacle.

discussion see Hickman, 1984). Enlargement of the first marginal is a character state of the Calliostomatinae, but other features of the radula and external anatomy of *Calliostoma* Swainson, 1840, are missing.

Cataegis new genus

Type species: *Cataegis toreuta* new species.

Diagnosis: Shell of moderate size (to about 25 mm in height), turbinate, slightly wider than high, non-umbilicate, with strong spiral sculpture; white under greenish-brown periostracum. Whorls well rounded, with about 7–12 strong, irregularly rugose or finely nodose spiral cords; axial sculpture of nodes or limited to strong growth lines; base rounded, aperture oblique, circular, nacreous within; outer lip thin, fluted by spiral sculpture; columella smooth, thickened, evenly arcuate. Operculum corneous, thin, circular, multispiral, with central nucleus.

Characters of gill, external anatomy, and radula as described above under subfamilial diagnosis.

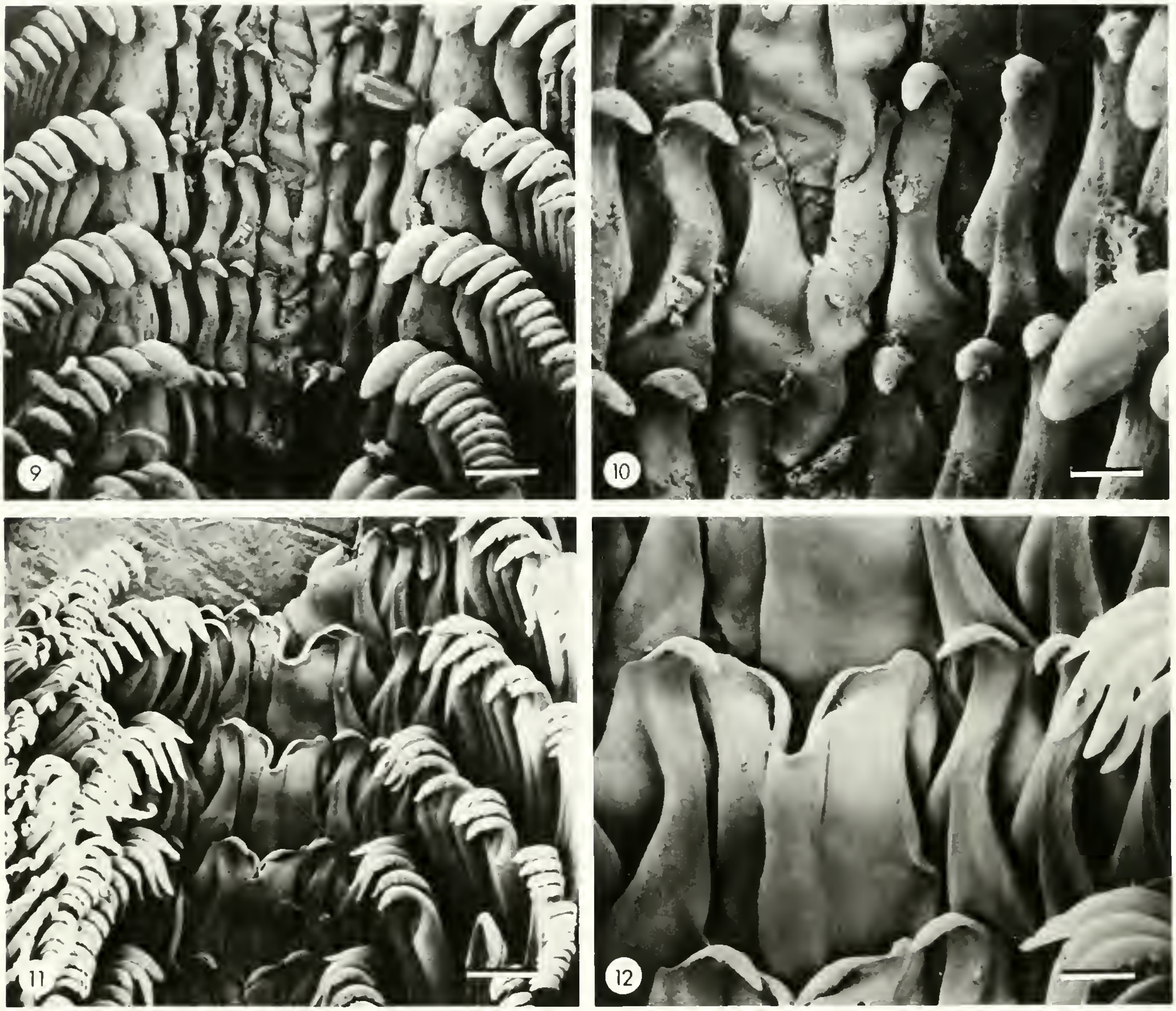
Distribution: *Cataegis* is known from the three new species here described: the type species *C. toreuta*, *C. meroglypta* (both known from contiguous continental slopes of the mainland extending from the Gulf of Mexico to Colombia), and *C. celebesensis* at similar depths from Indonesia. The existence of two Caribbean species plus *C. celebesensis* in the Indo-Pacific faunal province indicates that the distribution of the genus is Tethyan and at least Cretaceous in origin. Until continental slope depths of other regions of the world are adequately sampled, it is unknown whether the present distribution is that of a relict genus, although that is the most likely explanation. All records for this genus are from continental slope depths, suggesting that the genus survives in relatively deep water. This agrees with the conclusion of Jablonski *et al.* (1983) that evolutionary innovations arise in shallow water and survive extinction by retreating offshore to deeper water where conditions are more stable.

Gut contents of the specimen of *Cataegis toreuta* from which the radula was prepared (figures 9, 10) included numerous pieces of plant remains identified as the Caribbean turtle grass, *Thalassia testudinum*, remains of which are common in the deep sea and continental slopes (for review see Wolff, 1979). The ready availability of this food may be a factor relating to the relatively large size of members of the genus. It lends further support to the hypothesis that the group originated in shallow water, the source of the food supply.

Etymology: Latin *cataegis* (from Greek *kataigis*), a feminine noun meaning hurricane or whirlwind, with reference to the strong spiral sculpture.

Cataegis toreuta new species
(figures 1, 2, 6, 9, 10)

Description: Shell (figures 1, 2) attaining 24.6 mm in height, 25.1 mm in diameter, turbinate, non-umbilicate, rather thick and solid, white. Periostracum thin, deciduous, light brown. Protoconch diameter 400 μm. Teleoconch whorls 5, rapidly expanding, last whorl well rounded. Spiral sculpture of 8–12 (usually 9) strong cords with broad, strongly concave interspaces; interspaces with fine



Figures 9–12. Radulae of *Cataegis*, SEM micrographs. **9, 10.** *Cataegis toreuta* new species (sta. 71-A7-11), showing fused first laterals, second, third, and fourth laterals, enlarged first marginal and succeeding pairs of marginals (scale bar of 9 = 50 μm, of 10 = 20 μm). **11, 12.** *Cataegis celebesensis* new species (holotype), showing same features (scale bar of 11 = 50 μm, of 12 = 20 μm).

intercalary spiral threads. Axial sculpture on second and third whorls of regularly spaced, oblique folds forming sharp nodes on crossing primary spirals; third to fifth whorls with close-set, irregular collabral growth lines forming low, sublamellar nodes on primary spiral cords. Base not distinct from rest of whorl, with umbilical depression. Aperture nearly circular, nacreous within; outer lip strongly prosocline, fluted by external sculpture; columella arcuate, thickened, smooth, with thin wash of nacre; inner lip reflected, thickened, usually concealing umbilical depression; parietal wall with thin porcelaneous callus. Operculum corneous, thin, amber, multispiral with numerous volutions.

Dimensions: Holotype: height 21.8 mm, diameter 22.9 mm; largest specimen: height 24.6 mm, diameter 25.1 mm.

Gill and external anatomy (figure 6) as described above under subfamily diagnosis.

Radula (figures 9, 10) lacking rachidian; lateral teeth 4 pairs, first laterals fused at base, uncusped; second, third, and fourth laterals with simple, tapered, overhanging tips; shafts elongate with narrow frontal elements and large, triangular rear elements; inner edge of rear element interlocking with corresponding depression on outer edge of adjacent lateral tooth; latero-marginal plate not evident; marginals numerous, shaft of first marginal twice breadth of the second; second marginal twice thickness of third; remaining marginals decreasing in

size, with sickle-shaped tips and up to 6 blunt denticles on each side of tapered tip.

Type locality: W of Punta Piedras, Colombia, 9°20.2′N, 76°34.2′W, 933–961 m.

Type material: Holotype: USNM 784755, *John Elliott Pillsbury* sta. P-364, 10′ otter trawl, July 13, 1966 (figure 1). Paratypes (by vessel and station number):

John Elliott Pillsbury sta. P-381, off Colombia, 10°17′N, 75°59.9′W, 733–604 m; 2 specimens, UMML 30.3420; 2 specimens, LACM 2264.

John Elliott Pillsbury sta. P-388, off Colombia, 10°16′N, 76°03′W, 824–1,061 m; 1 specimen, UMML 30.3429.

John Elliott Pillsbury sta. P-394, off Colombia, 9°28.6′N, 76°26.3′W, 421–641 m; 4 specimens, UMML 30.3498.

John Elliott Pillsbury sta. P-407, off Colombia, 9°00.2′N, 77°25.3′W, 1,171–1,239 m; 3 specimens, USNM 784756; 2 specimens, MCZ 296111; 2 specimens, ASNP 359168; 2 specimens, FSBC I 31770; 2 specimens, UMML 30.3576.

John Elliott Pillsbury sta. P-413, off Colombia, 9°01.5′N, 76°53′W, 1,281–1,283 m; 3 specimens, UMML 30.3607.

Oregon II sta. 4580, off Biloxi, Mississippi, 29°06′N, 88°06′W, 805 m; 1 specimen, USNM 801816 (figure 2).

Oregon II sta. 11228, off Panama, 9°05′N, 81°18′W, 594 m; 7 specimens, FSM 28719.

Oregon II sta. 39554, off Corpus Christi, Texas, 27°25.7′N, 95°54.2′W, 337–412 m; 1 specimen, FSM 40669.

Alaminos sta. 68-A7-10A, off Pensacola, Florida, 29°15.5′N, 86°55′W, 541 m; 1 specimen, MNHN uncat.

Alaminos sta. 68-A7-15H, off Pensacola, Florida, 29°10.5′N, 87°16′W, 914 m; 1 specimen, MNHN uncat.

Alaminos sta. 69-A11-64, off Vera Cruz, Mexico, 19°28′N, 95°58′W, 384 m; 1 specimen, TAMU 4-1954.

Alaminos sta. 71-A7-11, off Brownsville, Texas, 26°32.3′N, 96°05′W, 636 m; 1 specimen, MNHN uncat. (figures 9, 10, radula).

Alaminos sta. 71-A8-47, off Vera Cruz, Mexico, 21°35′N, 96°54.6′W, 937 m; 1 specimen, MNHN uncat.

Distribution: Western Atlantic, off Pensacola, Florida, to Colombia, continental slope depths, 337–1,283 m.

Etymology: Greek *toreuta*, masculine noun in apposition, worker using a lathe.

Remarks: This is the best represented of the three species of *Cataegis*. It is the only species in which the nodose axial sculpture persists in later whorls. The radula differs from that of *C. celebesensis* in having the first marginals more prominent, and in more clearly indicating that the central element represents a fusion of the first lateral teeth (figure 10).

Cataegis meroglypta new species
(figures 3, 4, 7, 8)

Description: Shell (figures 3, 4) attaining at least 17.8 mm in height, 18.9 mm in diameter; turbinate, rather thick and solid, white. Periostracum thick, brown to greenish-brown. Protoconch unknown (eroded on all specimens). Teleoconch whorls 3.5, rapidly expanding, last whorl well rounded. Spiral sculpture of 4 or 5 strong spiral cords adapically and 6 or 7 on base; cords irregularly rugose, but not distinctly beaded; interspaces between primary spiral cords smooth or bearing as many as 5 weak spiral threads. Axial sculpture on first 2 whorls of low, oblique folds radiating from suture to first primary cord; later whorls with low, irregular, rugose, collabral growth lines. Base not distinct from rest of whorl, with central umbilical depression. Aperture nearly circular, nacreous within; outer lip strongly prosocline, slightly fluted by external spirals; columella arcuate, thickened, smooth, with thin wash of nacre; inner lip reflected, forming rather thick, porcelaneous callus concealing most of umbilical depression; parietal wall with thin wash of porcelaneous callus. Operculum corneous, thin, amber, multispiral with numerous volutions.

Dimensions: Holotype: height 17.8 mm, diameter 18.9 mm; paratype: height 16.9 mm, diameter 18.4 mm.

Gill and external anatomy (figures 7, 8) as described above under subfamily diagnosis.

Radula not examined (body of holotype maintained intact).

Type locality: S of Mississippi River Delta, Louisiana, 27°49′N, 90°07′W, 845–858 m.

Type material: Holotype: MNHN uncat., LGL Cruise I-MMS-C3 (figure 3). Paratypes (empty shells): *John Elliott Pillsbury* sta. P-394, W of Punta Piedras, Colombia, 9°28.6′N, 76°26.3′W, 421–641 m; 1 specimen, USNM 784757 (figure 4); 2 specimens + 1 fragment, UMML 30.3499.

Distribution: Western Atlantic; Louisiana to Colombia, continental slope depths, 421–858 m.

Etymology: Adjective derived from Greek: *meros*, part, and *glyptos*, carved.

Remarks: *Cataegis meroglypta* differs from *C. toreuta* new species in having fewer, weaker spiral cords that are irregularly rugose rather than discretely nodulose, weaker spiral threads between the adapical cords, and a thicker, darker periostracum.

Cataegis celebesensis new species
(figures 5, 11, 12)

Description: Shell (figure 5) attaining 20.4 mm in height, 20.3 mm in diameter, turbinate, non-umbilicate, rather thick and solid, white. Periostraeum thin, deciduous, light brown. Protoconch unknown (eroded in holotype). Teleoconch whorls 4, rapidly expanding, last whorl well rounded. Spiral sculpture of 8 strong cords with broad,

strongly concave interspaces; fine intercalary spiral threads present in interspaces. Axial sculpture of irregular rugosities on spiral cords and close-set, irregular collabral growth lines. Base not distinct from rest of whorl. Aperture nearly circular, nacreous within; outer lip strongly prosocline, fluted by external sculpture; columella arcuate, thickened, smooth, with thin wash of nacre; inner lip reflected, raised over umbilical depression; parietal wall with thin porcelaneous callus. Operculum corneous, thin, amber, multispiral with numerous volutions.

Dimensions: Holotype: height 20.4 mm, diameter 20.3 mm.

Gill and external anatomy as described above under subfamily diagnosis.

Radula (figures 11, 12) lacking rachidian; lateral teeth 4 pairs, inner laterals uncusped, fused at base, fused area buckling forward; second, third, and fourth laterals with simple, tapering, overhanging cusps; shafts elongate with narrow elements and larger, triangular rear elements; inner edge of rear element interlocking with corresponding depression on outer edge of adjacent lateral tooth; latero-marginal plate not evident; marginals numerous, innermost marginals slightly larger than remaining marginals, with sickle-shaped tips and up to 6 blunt denticles on each side of tip.

Type locality: Makassar Strait, off W side Minahassa Peninsula, Celebes, Indonesia, 0°05′S, 119°48′E, 1,080 m.

Type material: Holotype: MNHN uncat., Corindon Expedition sta. 231 (figure 5). Paratype (dry with operculum in place): *Albatross* sta. 5668, Makassar Strait, Indonesia, 2°28′S, 118°49′E, 1,647 m; 1 specimen, USNM 239507.

Distribution: Makassar Strait, Indonesia, 1,080–1,647 m.

Etymology: The name is an adjective derived from Celebes Island.

Remarks: *Cataegis celebesensis* differs from *C. toreuta* in having a higher profile of fewer whorls and in lacking the pronounced axial nodes of that species. The radula of *C. celebesensis* has first marginals that are not as enlarged as those of *C. toreuta*. The illustrated preparation of the radula of the holotype shows the fused first lateral teeth in nearly perfect condition (figure 12). The regular outline of the first laterals in successive rows shows that cusps were not formed and eliminates the possibility that the cusps were simply worn down.

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LITERATURE CITED

Hickman, C. S. 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. Malacologia 25:143–160.

Jablonski, D., J. J. Sepkoski, Jr., D. J. Bottjer, and P. M. Sheehan. 1983. Onshore-offshore patterns in the evolution of Phanerozoic shelf communities. Science 222:1123–1125.

Keen, A. M. 1960. [Cenozoic Archaeogastropoda.] *In:* Moore, R. C. (ed.). Treatise on invertebrate paleontology. Part I, Mollusca 1, Geological Society of America and University of Kansas Press, Lawrence, xii + 351 p.

Marshall, B. A. 1979. The Trochidae and Turbinidae of the Kermadec Ridge (Mollusca: Gastropoda). New Zealand Journal of Zoology 6:521–552.

McLean, J. H. 1982. Importance of gill structure in trochacean classification. The Western Society of Malacologists. Annual Report 14:11.

Wolff, T. 1979. Macrofaunal utilization of plant remains in the deep sea. Sarsia 64:117–136.

Significance of Radular Characters in Reconstruction of Thaidid Phylogeny (Neogastropoda: Muricacea)

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ABSTRACT

Radulae of 16 species representing nine thaidid genera were examined using scanning electron microscopy. Radular characters of thaidid gastropods are incongruent with existing taxonomic schemes based on conchology, but highly congruent with phylogenetic schemes based on anatomy, and seem to be evolutionarily conservative. Correlation analyses of the relationship between radular morphology and diet were done to determine if radular morphology is indicative of the type of food eaten. Results show no significant correlation between the two variables. Congruence of radular morphology with a classification based on anatomical data, and the absence of correlation between radular morphology and diet, are evidence that radular characters are valid indicators of phylogeny for thaidid gastropods. Furthermore, the data suggest that diet does not present a strong selective force in the evolution of radular morphology in thaidid gastropods.

INTRODUCTION

Thaidid gastropods comprise a conglomerate of disparate muricid taxa, inhabiting mostly intertidal epifaunal habitats in temperate and tropical regions. Considerable instability exists in the supraspecific classification in this group. Some authors (Keen, 1971a,b; Radwin & D'Attilio, 1971, 1972, 1976; Golikov & Starobogatov, 1975; Harasewych, 1984) accord familial rank to this group (Thaididae Jousseaume, 1888). Others (Cernohorsky, 1969, 1982, 1983; Emerson & Cernohorsky, 1973; Ponder, 1973; Abbott, 1974; Fujioka, 1985) treat it as a subfamily (Thaidinae Suter, 1913, less commonly as Purpurinae Menke, 1828) of Muricidae Rafinesque, 1815. Preliminary anatomical investigations suggest a subfamilial status for this group (Kool, in preparation).

All classifications of thaidid taxa to date are reliant on shell morphology (Reeve, 1846; Thiele, 1929; Wenz, 1941; Keen, unpublished manuscript). A number of authors (Colton, 1922; Moore, 1936; Hoxmark, 1971; Kitching & Lockwood, 1974; Balaparameswara Rao & Bhavanarayana, 1976; Spight, 1976; Vermeij, 1979; Vermeij & Currey, 1980; Crothers, 1983) have reported on the considerable effects of environmental influences on thaidid shell morphology. Comparisons of classifications based on shell morphology with those based on anatomical characters (Kool, 1986a,c, and in preparation), have revealed convergence in shell morphology, and suggest that classifications based solely on conchological characters are unreliable.

Many authors (Troschel, 1856–93; Cooke, 1919; Thiele, 1929; Clench, 1947; Arakawa, 1962, 1964; Radwin & Wells, 1968; Wu, 1968, 1973, 1985; Radwin & D'Attilio, 1971, 1972, 1976; Emerson & Cernohorsky, 1973; Bandel, 1984; Harasewych, 1984; Fujioka, 1985) have proposed or discussed classifications of the thaidids, based on radular and conchological characters. Many of these authors have discussed cases of incongruence between classifications based on shell shape and those based on radular morphology. Different radular morphologies have been found in congeneric species, while similar radulae frequently occur in different genera. A lack of congruence between classifications based on shell shape and those based on radular characters may be due to convergence in shell shape or convergence in radular morphology, perhaps determined by diet, or differential divergence.

The purpose of this study is three-fold. In the first section, a classification based on radular characters is compared with one based on anatomical data. Congruence between a generic classification based on anatomy (not on radular data) and a scheme based on radular characters, may indicate that radular characters are valid indicators of phylogeny rather than manifestations of an external selective pressure such as diet (Kool, 1986b:233).

In the second part of this paper, overall correlation is measured between radular morphology and diet by calculation of correlation coefficients for the total data set as well as several subsets.

Thirdly, all species pairs were divided into nine arbitrarily set categories based on radular and dietary similarities to detect patterns of relationship between radular morphology and diet. Detection and quantification of similarity other than similarity by descent (*i.e.*, convergence) is possible by differentiating pairs of congeners from pairs of intergeners. The degree of congruence between radular and dietary similarities in pairs of congeners and intergeners may provide insight into the role

Table 1. Radular characters used in correlation studies and cladistic analysis. Character states followed by reference to illustrative figure.

1) Central cusp (cc) morphology
   - a = triangular elongated, wide base (figure 10)
   - b = thin, needle shaped (figure 13)
   - c = base constricted (figure 40)
   - d = triangular, flap-like, base extremely wide (figure 31)
2) Longitudinal cavity in central cusp:
   - a = absent (figure 46)
   - b = present (figure 49)
3) Denticle between central and lateral cusp (lc):
   - a = present (1d), separate from central and lateral cusp (figure 42)
   - b = present (idlc), high on lateral cusp (figure 34)
   - c = present (idlc), low on lateral cusp (figure 4)
   - d = absent (figure 31)
4) Lateral cusp orientation:
   - a = pointing outward, outer edge concave (figure 49)
   - b = straight, or slightly inward (figure 13)
5) Outer denticle(s) on lateral cusp:
   - a = absent (figure 46)
   - b = present as low serrations (lcs) (figure 7)
   - c = present, single (odlc) (figure 25)
   - d = present as long distinct denticles (figure 16)
6) Area between lateral cusp and side of rachidian:
   - a = small, sloping down towards outside (figure 52)
   - b = wide, horizontal (figure 46)
7) Marginal denticles (md):
   - a = absent (figure 46)
   - b = present, distinct, elongated (figure 40)
8) Position of lateral cusp relative to marginal edge:
   - a = lateral cusp and marginal edge oriented in similar direction (not figured)
   - b = lateral cusp and marginal edge oriented in different directions (not figured)
9) Marginal cusp (mc):
   - a = absent (figure 46)
   - b = present, well defined, about the size of marginal denticles (figure 25)
   - c = present, distinctly longer and more robust than marginal denticles (figure 37)
   - d = very small and inconspicuous
10) Lateral extension of rachidian base:
   - a = absent (figure 49)
   - b = present, elongated (figure 7)
   - c = present as small lateral protrusion (figure 34)
11) Lateral tooth:
   - a = smooth (figure 33)
   - b = serrated at base (figure 30)
12) Lateral tooth length:
   - a = longer than rachidian width (figure 30)
   - b = equal to rachidian width (figure 36)
   - c = shorter than rachidian width, but longer than ½ rachidian length (figure 21)
   - d = shorter than ½ rachidian width (figure 24)

diet may play on the evolution of radular morphology. For example, if a high degree of such correspondence is found between intergeneric species pairs, the hypothesis that diet has had significant influence on the evolution of radular morphology is plausible; an absence of correlation between radular and dietary similarities in pairs of intergeners may indicate that diet has not contributed detectably to radular morphology.

Thaidid gastropods are very suitable for correlation studies between radular morphology and anatomy, and radular morphology and diet, because the necessary data are readily available. Additionally, substantial interspecific variation in diets and radulae facilitate detection of correlation patterns (if present) between radular morphology and diet.

MATERIALS AND METHODS

Radular data are based on the following specimens (numbers in parentheses indicate number of individuals):

Nucella lapillus (Linné, 1758): (3) Kittery, Maine, USA, USNM No. 836050; (3) Pemaquid Point, Maine, USA, USNM No. 857053

Nucella lamellosa (Gmelin, 1791): (4) Deception Pass, Fidalgo Island, Puget Sound, Washington, USA, USNM No. 841242

Nucella emarginata (Deshayes, 1839): (5) Bamfield, British Columbia, Canada, NMNH No. 857054

Concholepas concholepas (Bruguière, 1789): (2) Valparaiso, Chile, USNM No. 857055

Plicopurpura patula (Linné, 1758): (5) South Miami Beach Inlet, Florida, USA, USNM No. 857056

Drupella cornus (Röding, 1798): (2) Pago Bay, Guam, USA, USNM No. 857057

Vexilla vexillum (Gmelin, 1791): (2) Pupukea Beach, Oahu, Hawaii, USA, USNM No. 836956

Morula uva (Röding, 1798): (3) Pago Bay, Guam, USA, USNM No. 857058

Morula granulata (Duclos, 1832): (2) Magnetic Island, Queensland, Australia, USNM No. 842658

Drupa morum Röding, 1798: (4) Pago Bay, Guam, USA, USNM No. 857059

Drupa rubusidaeus Röding, 1798: (2) Pago Bay, Guam, USA, USNM No. 857060

Drupa ricinus (Linné, 1758): (3) Pago Bay, Guam, USA, USNM No. 857061

Drupa grossularia Röding, 1798: (2) Pago Bay, Guam, USA, USNM No. 857062

Stramonita haemastoma (Linné, 1767): (4) Sebastian Inlet, Sebastian, Florida, USA, USNM No. 857062

Purpura panama Röding, 1798: (2) Salt Rock, Natal, South Africa, South African Museum

Purpura harpa Conrad, 1837: (3) Makapuu, Oahu, Hawaii, USA, USNM No. 836958

Muricanthus fulvescens (Sowerby, 1834): (2) Cape Canaveral, Florida, USA, USNM No. 857064

Muricanthus fulvescens is a representative of the subfamily Muricinae, a sister group of the thaidids, and is used as an outgroup in the cladistic analysis. Some of the generic reallocations of the above species have been published; *Nucella* Röding, 1798, and *Stramonita* Schu-

macher, 1817, are anatomically very distinct from *Thais* Röding, 1798 (Kool 1986a:110, and in preparation). *Plicopurpura* Cossmann, 1903, is very different from *Purpura* Bruguière, 1789, in its anatomy (Kool, 1986a:110, and in preparation). The nominal thaidid species *harpa* seems thus far to be closely linked with *Purpura sensu stricto*. Recognition of other thaidid genera used herein (*Morula* Schumacher, 1817, *Drupa* Röding, 1798, *Vexilla* Swainson, 1840, *Drupella* Thiele, 1925, and *Concholepas* Lamarck, 1801) is based on anatomical data (*i.e.*, exclusive of radula) also.

Radulae (two to six per species) were dissected from live and preserved animals, cleaned in KOH, and examined using a variety of scanning electron microscopes. Four micrographs were taken of the central portion of each radular ribbon. The first two photographs (one including lateral teeth, one excluding lateral teeth) were taken perpendicular to the radular ribbon. The radula was tilted laterally to an angle of 40 degrees for a third photograph, to obtain a lateral view of the cusp and denticle morphology of the rachidian tooth. Finally, the radula was tilted laterally to an angle of about 85 degrees for a fourth photograph, used to examine the edge of the rachidian tooth and the angles, sizes, and locations of its cusps and denticles.

Characters and character states, derived from analysis of these photomicrographs, are presented in table 1. Intra-specific variation was not assessed, as only several specimens of each species were examined.

Terminology used for the cusps and denticles of the rachidian tooth (figure 1) is largely taken from Fujioka (1985), with the following modifications. The term "outer denticles" (odlc) is used herein to describe only the denticle(s) on the outer side of the lateral cusp. The term "lateral cusp serration" (lcs) is chosen herein to describe a series of small denticles on the outer side of the lateral cusp, which are homologous with the outer denticle(s) (odlc). Denticles on the outer side of the lateral cusp, but separated from it, are here called "marginal denticles" (md). A distinction is also made between an inner denticle on the lateral cusp (idlc), and a lateral denticle (ld), which is free of the lateral cusp, but is homologous with the inner denticle. Some subjectivity is involved in determining when denticles can be deemed free of the lateral cusp.

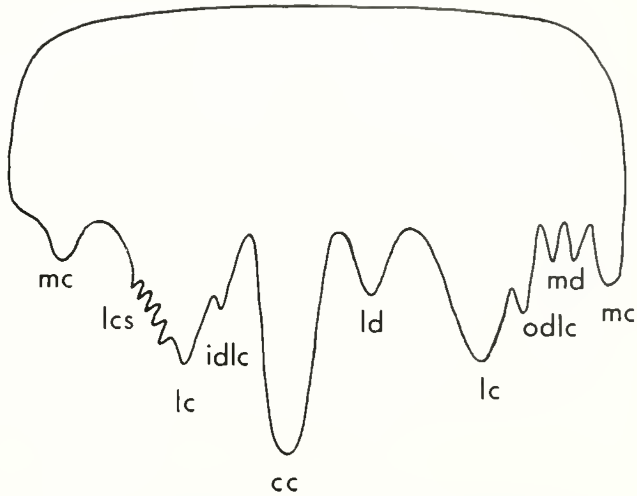


Figure 1. Schematic drawing of composite thaidid rachidian tooth. mc = marginal cusp, md = marginal denticle, lcs = lateral cusp serration, lc = lateral cusp, idlc = inner denticle on lateral cusp, cc = central cusp, ld = lateral denticle (homologous with idlc), odlc = outer denticle on lateral cusp (homologous with lcs).

Table 2. Character matrix (see table 1) for taxa used in correlation studies and cladistic analysis.

	Characters and character states											
Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Nucella lapillus	b	a	c	b	b	a	a	b	b	b	a	c
Nucella emarginata	b	a	b	b	b	a	a	a	b	b	a	c
Nucella lamellosa	b	a	c	b	b	a	a	b	b	b	a	c
Plicopurpura patula	b	b	a	a	a	a	a	a	a	a	a	a
Concholepas concholepas	a	a	b	a	b	a	a	a	d	a	a	a
Vexilla vexillum	d	a	d	b	a	a	a	a	a	a	b	a
Morula granulata	b	a	a	b	a	b	a	a	a	a	a	c
Morula uva	b	a	a	b	a	b	b	a	b	a	a	c
Drupa morum	b	a	c	b	d	b	b	a	c	a	a	c
Drupa ricinus	b	a	b	b	c	b	b	a	b	a	a	c
Drupa rubusidaeus	b	a	c	b	a	b	b	a	b	a	a	c
Drupa grossularia	c	a	b	b	c	b	b	a	b	c	a	d
Purpura harpa	c	a	c	b	c	b	b	a	c	c	a	b
Purpura panama	c	a	c	b	c	b	b	a	c	c	a	b
Stramonita haemastoma	c	a	b	b	b	a	a	a	b	c	a	b
Drupella cornus	d	a	a	b	b	a	a	a	a	a	b	a
Muricanthus fulvescens[1]	a	a	a	a	a	a	a	a	a	a	a	a

[1] Outgroup in cladistic analysis; not used in correlation studies.

Table 3. Sources of information on thaidid diets.

Taxon	Authors
Nucella lapillus	Connell, 1961; Crothers, 1985; Largen, 1967; Menge, 1978; Moore, 1936
Nucella emarginata	Connell, 1970; Emlen, 1966; Kool, personal observation; Spight, 1979, 1982; Suchanek, 1978
Nucella lamellosa	Connell, 1970; Spight, 1979, 1982; Suchanek, 1978
Concholepas concholepas	Gallardo, 1979
Plicopurpura patula	Bandel, 1984; Clench, 1947; Kool, personal observation
Purpura panama	Taylor, 1971, 1976
Purpura harpa	Kay, 1979; Kool, personal observation
Drupa morum	Bernstein, 1974, Kay, 1971, 1979; Taylor, 1968, 1983, 1984; Thomas and Kohn, 1985
Drupa ricinus	Bernstein, 1974, Kay, 1971; Taylor, 1976, 1978, 1983, 1984; Thomas and Kohn, 1985; Wu, 1965a
Drupa rubusidaeus	Taylor, 1983
Drupa grossularia	Taylor, 1983, 1984
Stramonita haemastoma	Butler, 1985; Cake, 1983; Gunter, 1979; Kool, personal observation; St. Amant, 1938
Morula uva	Kay, 1971; Miller 1970; Taylor, 1976, 1984
Morula granulata	Bernstein, 1974, Kay, 1979; Kool, personal observation; Miller, 1970; Taylor, 1968, 1971, 1976; Wu, 1965a
Drupella cornus	Demond, 1957; Kay, 1979; Kool, personal observation; Robertson, 1970, Taylor, 1976, 1978
Vexilla vexillum	Kay, 1979; Kool, personal observation

Dietary data were obtained from the literature as well as from personal field observations (table 3). Prey items were categorized as follows: (1) shelled mollusks, (2) barnacles, (3) other small crustaceans, (4) errant polychaetes, (5) coral polyps, (6) echinoids, (7) holothurians, and (8) sponges. No separate category was established for tubiculous polychaetes or sipunculans (eaten by very few species in this analysis), which were included with shelled mollusks and errant polychaetes, respectively, based on similarity in outer body coverings.

Twelve radular characters, comprising 35 character states (tables 1, 2), were employed for a cladistic analysis using PHYSYS (Farris & Mickevich, copyright 1985). *Muricanthus fulvescens* was used as an outgroup to polarize character states. Multistate characters were kept "unordered" so that any unique character state could be derived directly from the ancestral state. No further *a priori* assumptions were made about transformation series. Dietary items were superimposed on the cladogram, to examine possible correlation between evolution of radular morphology and dietary patterns.

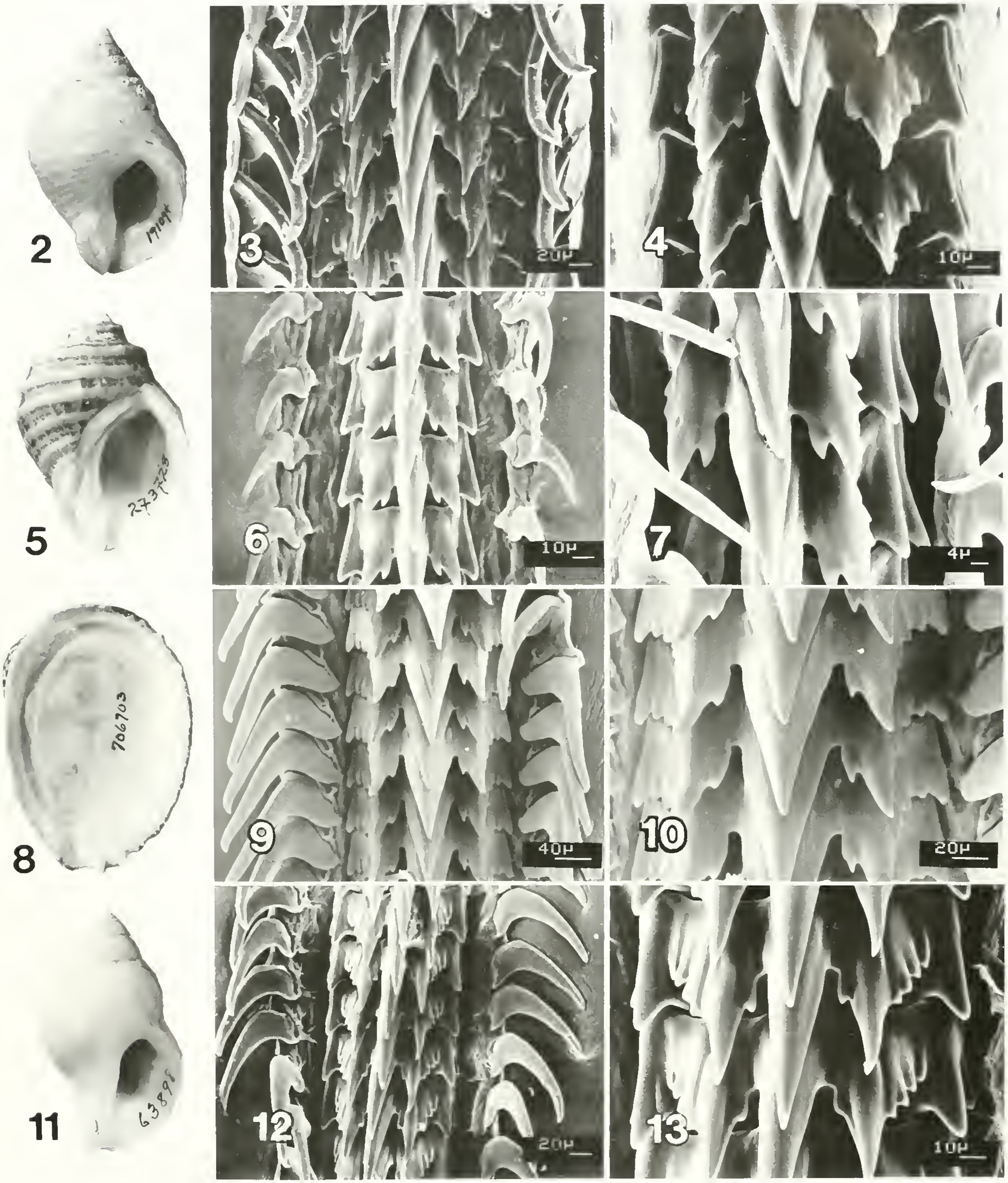
Two similarity coefficients were calculated for each possible pairwise comparison between species, one based on radular morphology, one based on diet. These similarity coefficients were then used to calculate a correlation coefficient between radular and dietary similarities.

The number of positive radular character state matches were divided by the number of characters (12). Thus, 13 different values for the radular similarity coefficient were theoretically possible. Although a binary (presence/absence) coding method appeared to be the best way to treat dietary data, it did not allow differentiation between "main" and "supplemental" food items. A quantitative factor was introduced by scoring main food items "11", supplemental prey "01", and excluded food items "00". The coefficient of Jaccard (Sneath & Sokal, 1973: 131) was then used to calculate dietary similarity between species. This similarity coefficient seemed most appropriate, because it disregards negative (0-0) matches, which are based on the absence of a food item in the diets of both taxa. The relative terms "main" and "supplemental" were arbitrarily derived from quantitative studies in the literature: prey was considered "supplemental" if eaten as a very small percentage (< 10%) in relation to the main food item. Data from non-quantitative studies required more subjective interpretations. Terms such as "were occasionally eaten" or "in one instance" assisted in these interpretations. More precise quantification of diet was impossible due to the variety of ways in which feeding data are presented in the literature.

Thus, if one species feeds on mollusks but not on barnacles, and another feeds rarely on mollusks, but mainly on barnacles, the scoring patterns would be 11-00 and 01-11, respectively. A comparison of these species would produce a similarity coefficient of 1/4, or 0.25. A comparison between species scored as 11-00 and 01-00 would result in a similarity coefficient of 1/2, or 0.50, since the two negative matches are not taken into consideration.

A Pearson correlation coefficient (Siegel, 1956:195) was calculated based on the similarity coefficients of thaidid diet and radular morphology using SYSTAT (Wilkinson, 1986). This analysis was also performed on three subsets of the total number of pairwise comparisons. One analyzed only of pairs of congeners; another analyzed only pairs of intergeners. In a third subset, all pairwise comparisons with a dietary similarity of 0.00 were eliminated from the analysis.

In this study, the similarity coefficients for both radular morphology and diet were considered to fall into one of three arbitrarily set categories: high similarity (similar; coefficient > 0.62), median or equivocal similarity (coefficient between 0.62 and 0.37), and low similarity (dissimilar; coefficient < 0.37). Relationships between similarities of radular morphology and diet thus fell into one of nine possible categories.



Figures 2–4. *Nucella lapillus.* **2.** Shell 1.22 ×. **3.** Radula **4.** Rachidian. **Figures 5–7.** *Nucella emarginata.* **5.** Shell 1.44 ×. **6.** Radula. **7.** Rachidian. **Figures 8–10.** *Concholepas concholepas.* **8.** Shell 0.90 ×. **9.** Radula. **10.** Rachidian. **Figures 11–13.** *Nucella lamellosa.* **11.** Shell 1.06 ×. **12.** Radula **13.** Rachidian.

RESULTS

Figure 53 represents one of 13 equally parsimonious trees (consistency index = 0.56) produced using only radular data. Differences among trees were minor (see Discussion), and the number next to each bracket indicates the number of trees in which the bracketed portion appears. Generic assignment of the terminal taxa is based on previous cladistic analyses of these taxa using only anatomical data (*i.e.*, exclusive of radula).

The Pearson correlation coefficient between radular similarity and dietary similarity for all pairwise comparisons was 0.05. This coefficient was 0.31 for the analysis of the subset consisting of the 11 pairwise comparisons between congeneric species. It was −0.08 for the analysis of the subset consisting of all comparisons between intergeners, and −0.12 using the data set from which comparisons with 0.00 dietary similarity were excluded. No significant correlation ($|p| > 0.1$) between radular morphology and diet was found in any of these analyses, indicating that there is little or no correlation between diet and radular morphology in these taxa.

Similarity coefficients falling into the highest category (figure 54, Cell 1) for both radula and diet are present in only five out of the 120 pairwise comparisons. Two of these are comparisons between intergeners, the other three are comparisons between congeners. Another six congeneric and 13 intergeneric species pairs have radular similarities greater than 0.62 (figure 54, Cells 2, 3). Of these, three congeneric and 12 intergeneric species pairs have dissimilar diets, seven of the latter having a dietary similarity of 0.00. Eighty-two percent of all pairwise comparisons between congeners have high radular similarities. Of these, only one-third have a high similarity in diet. A mere 15 of the 106 comparisons (14%) between intergeneric species have high radular similarity. Only two of these have a high similarity in diet.

In six of the 11 comparisons between congeners, dietary similarity coefficients were lower than radular similarity coefficients, while radulae were less similar than diets in four comparisons. *Nucella lamellosa* (figures 11–13) and *N. lapillus* (figures 2–4) were exceptional in having identical radulae and diets.

In Cell 1, three of the five comparisons that show high similarity in both radula and diet occur between congeneric species. *Nucella lapillus*, *N. emarginata* (figures 5–7), and *N. lamellosa* all feed on barnacles and mollusks, and their radulae are much alike. *Stramonita haemastoma* (figures 32–34) and *Nucella emarginata* both feed on mollusks and barnacles, and have a radular similarity coefficient of 0.75. Similarly, *Plicopurpura patula* (figures 47–49) and *Morula granulata* (figures 44–46) have high similarities for both radula and diet.

The three pairs of congeners with high radular similarity corresponding with low dietary similarity (Cell 3), are all in the genus *Drupa*, which has the highest diversity in diet of all genera dealt with in this paper (see figure 53). Ten of the 12 intergeneric species pairs contain members of the genera *Drupa*, *Morula*, and *Purpura*, several having a dietary similarity coefficient of 0.00. The radula of *Drupa grossularia* (figures 23–25) is very similar to the radulae of *Purpura harpa* (0.75) (figures 38–40) and *P. panama* (0.75) (figures 35–37), even though there is no overlap of diets. *Drupella cornus* (figures 26–28), which feeds exclusively on coral polyps, and *Vexilla vexillum* (figures 29–31), an urchin feeder, also have very similar radulae (0.83).

Cell 5 contains the remaining two species comparisons between congeners: *Drupa morum* (figures 14–16) and *Drupa grossularia*. No two congeners were found to have coefficients for radular and dietary similarity lower than 0.50.

Representatives of Cell 6 show a moderate degree of resemblance in radular morphology, but little or no similarity in diet. This cell has the largest number of representatives of all nine cells.

Cell 7 contains 10 representatives, indicating that low radular similarity can exist between species with highly similar diets. All members of *Nucella*, *Purpura panama*, and *Plicopurpura patula* feed on mollusks and barnacles, resulting in a 1.00 dietary similarity coefficient for all pairwise comparisons between these taxa. However, the radular similarity coefficient between any *Nucella* species and either *Purpura panama* or *Plicopurpura patula* is only 0.33.

Cell 9 contains examples of species pairs with dissim-

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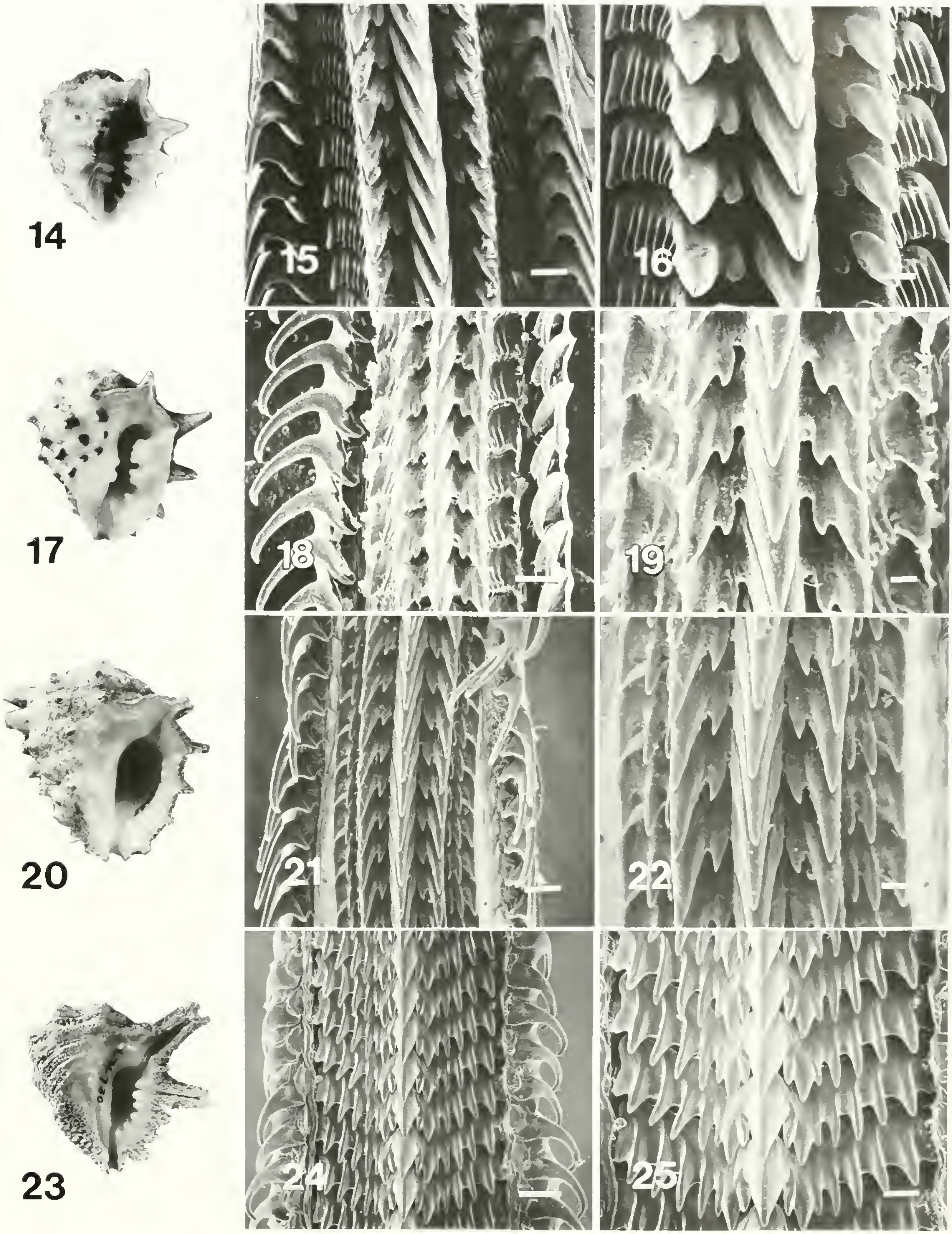
Figures 14–16. *Drupa amorum.* **14.** Shell 0.87 ×. **15.** Radula. Scale bar = 25 μm. **16.** Rachidian. Scale bar = 15 μm. **Figures 17–19.** *Drupa ricinus.* **17.** Shell 1.17 ×. **18.** Radula. Scale bar = 25 μm. **19.** Rachidian. Scale bar = 10 μm. **Figures 20–22.** *Drupa rubusidaeus.* **20.** Shell 0.89 ×. **21.** Radula. Scale bar = 25 μm. **22.** Rachidian. Scale bar = 10 μm. **Figures 23–25.** *Drupa grossularia.* **23.** Shell 1.25 ×. **24.** Radula. Scale bar = 20 μm. **25.** Rachidian. Scale bar = 10 μm.

Figures 26–28. *Drupella cornus.* **26.** Shell 1.14 ×. **27.** Radula. Scale bar = 0.1 mm. **28.** Rachidian. Scale bar = 10 μm. **Figures 29–31.** *Vexilla vexillum.* **29.** Shell 1.68 ×. **30.** Radula. Scale bar = 20 μm. **31.** Rachidian. Scale bar = 10 μm. **Figures 32–34.** *Stramonita haemastoma.* **32.** Shell 1.18 ×. **33.** Radula. Scale bar = 30 μm. **34.** Rachidian. Scale bar = 15 μm. **Figures 35–37.** *Purpura panama.* **35.** Shell 0.66 ×. **36.** Radula. Scale bar = 100 μm. **37.** Rachidian. Scale bar = 30 μm. **Figures 38–40.** *Purpura harpa.* **38.** Shell 1.45 ×. **39.** Radula. Scale bar = 30 μm. **40.** Rachidian. Scale bar = 15 μm.

Figures 41–43. *Morula uva.* **41.** Shell 1.50 ×. **42.** Radula. Scale bar = 10 μm. **43.** Rachidian. Scale bar = 10 μm. **Figures 44–46.** *Morula granulata.* **44.** Shell 1.33 ×. **45.** Radula. Scale bar = 40 μm. **46.** Rachidian. Scale bar = 30 μm. **Figures 47–49.** *Plicopurpura patula.* **47.** Shell 0.62 ×. **48.** Radula. Scale bar = 25 μm. **49.** Rachidian. Scale bar = 15 μm. **Figures 50–52.** *Muricanthus fulvescens.* **50.** Shell 0.37 ×. **51.** Radula. Scale bar = 50 μm. **52.** Rachidian. Scale bar = 20 μm.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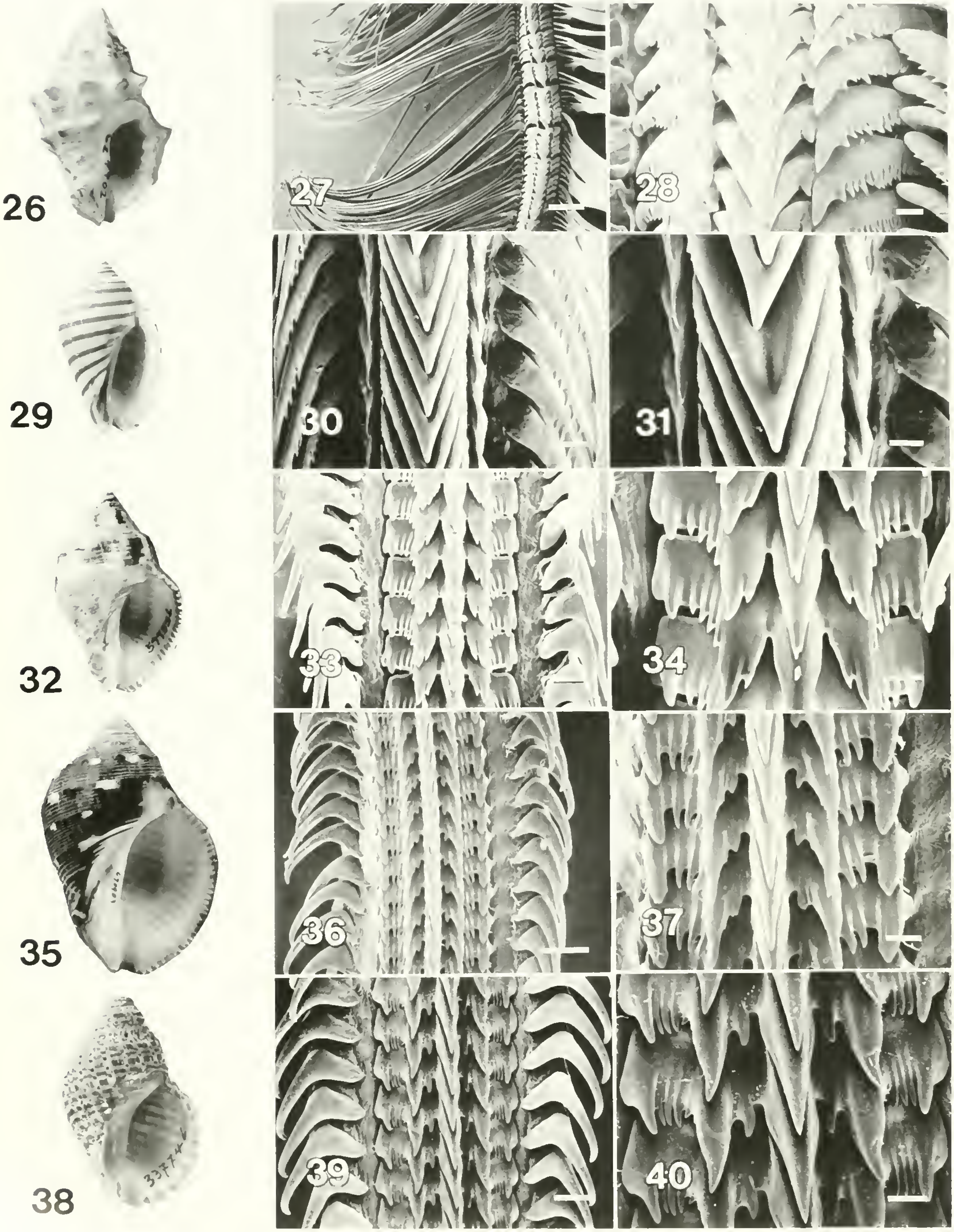
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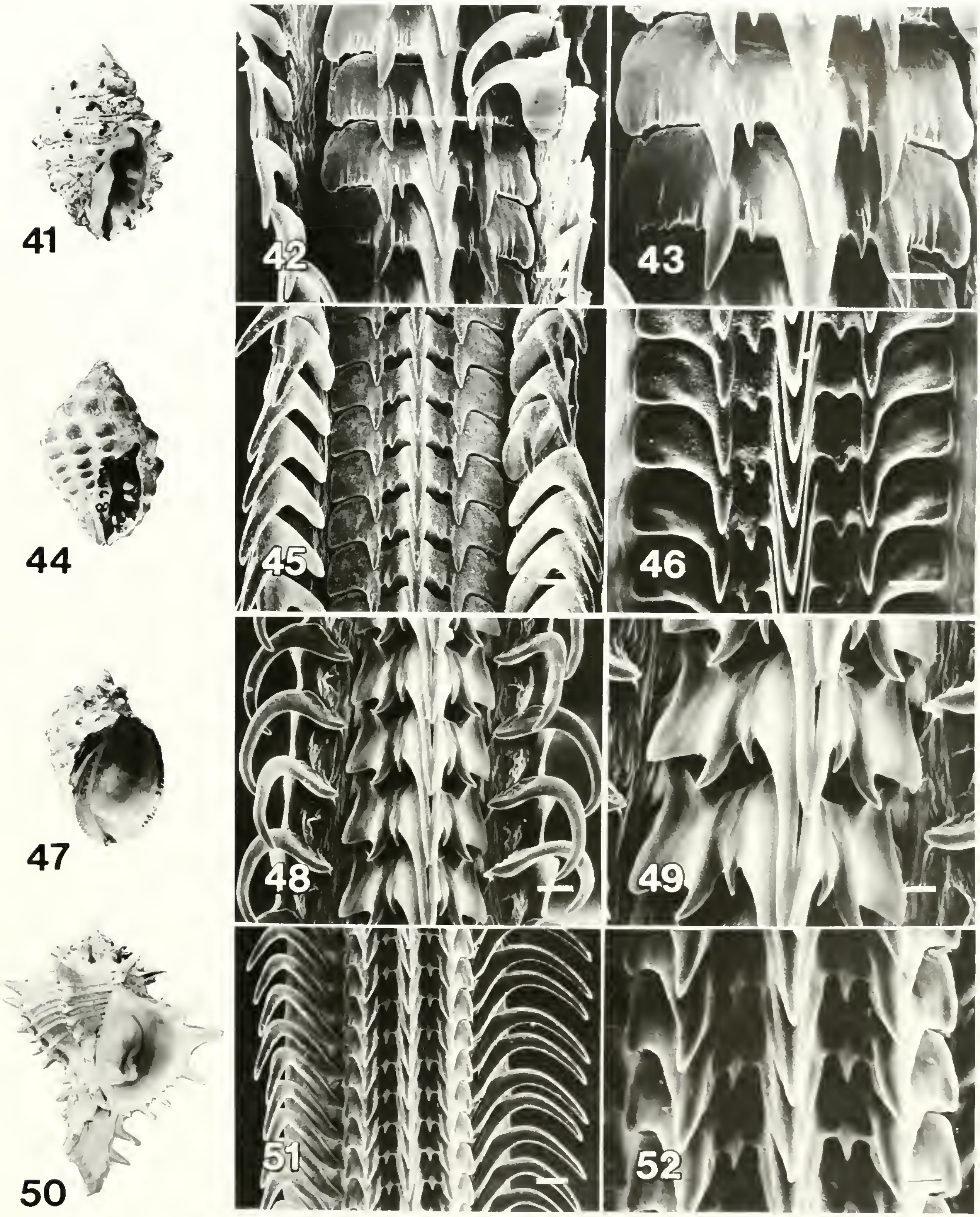
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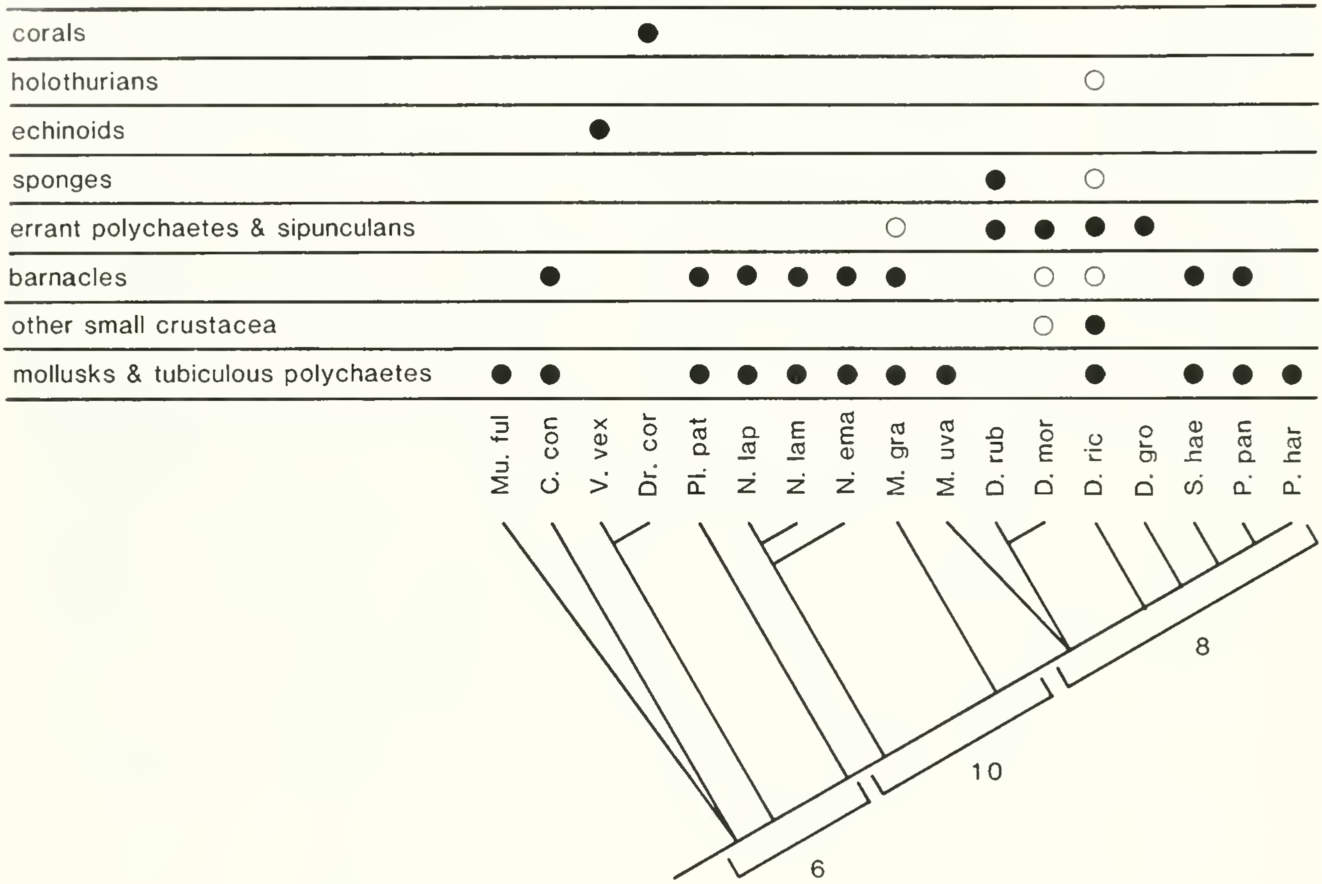

Figure 53. One of 13 equally parsimonious cladograms based on the radular characters in Table 1. Numbers below brackets indicate the number of trees in which the bracketed portion of the cladogram was identical. Prey eaten by each species is categorized into one or more groups and superimposed above each taxon. Solid circles indicate main food items, open circles indicate occasional prey. Mu. ful = *Muricanthus fulvescens*; C. con = *Concholepas concholepas*; V. vex = *Vexilla vexillum*, Dr. cor = *Drupella cornus*; Pl. pat = *Plicopurpura patula*; N. lap = *Nucella lapillus*; N. lam = *Nucella lamellosa*; N. ema = *Nucella emarginata*; M. gra = *Morula granulata*; M. uva = *Morula uva*; D. rub = *Drupa rubusidacus*; D. mor = *Drupa morum*; D. ric = *Drupa ricinus*; D. gro = *Drupa grossularia*; S. hae = *Stramonita haemastoma*; P. pan = *Purpura panama*; P. har = *Purpura harpa*.

ilar radulae and diets. Most of the comparisons in this cell involve at least one species with a highly specialized diet, such as *Vexilla vexillum*, *Drupella cornus*, and *Drupa grossularia* (sipunculan-feeder). These have little or no dietary overlap with species of other genera, and their radulae are distinct.

DISCUSSION

Results indicate high congruence between anatomy and radular morphology and absence of correlation between radular morphology and diet. The absence of overall correlation, combined with the paucity of defendable cases for which convergence, perhaps due to diet, could be invoked, suggest that the role of diet on evolution of radular morphology is insignificant.

The cladogram in figure 53 is not completely congruent with the classification based on anatomical data, differing in the following ways. The genera *Morula* and *Drupa*, which appear to be paraphyletic based on radular data alone, are, although closely related, each monophyletic based on anatomy (Kool, in preparation). The polytomy at the base of the tree is less reflective of phylogenetic relationship. Two polychotomies are present in all 13 trees and occur in the same regions as in the figured tree. Additional radular characters may provide higher resolution. Minor differences in resolution of the paraphyly of *Drupa* and *Morula* and switches in the position of *Plicopurpura patula* (branching off before the *Drupella*-*Vexilla* lineage) and *Morula granulata* (branching off before the *Nucella* clade) account for the variation among the 13 trees.

The high degree of congruence between a cladogram based on radular characters, and a generic division based on anatomy shows that radular characters are valuable indicators of phylogenetic relationship in thaidid gastropods, assuming anatomical data truly reflect this relationship. If dietary preference is superimposed on this

cladogram (or any of the other trees mentioned above), there is no gradient in food items consistent with the phylogenetic arrangement based on radular morphology. Taxa feeding on mollusks and barnacles, for example, are dispersed over the entire tree, suggesting that no correlation exists between diet and radular morphology.

The Pearson correlation coefficients for the total number of pairwise comparisons and for the subsets reveal no significant correlation between radular morphology and diet. Although the correlation coefficient is non-significant for all data sets, it is highest for the subset consisting of pairs of congeners. Similarity in radular morphology in these pairs is most likely due to close phylogenetic affinities, but it is possible that diet may have had some influence on it.

Diet may indeed affect radular morphology. However, prior to invoking adaptive scenarios and speculating about the influence of diet on the evolution of radular morphology in thaidid and other gastropods, a purely descriptive-correlative study between radular morphology and diet is necessary. If, for instance, several different radular types can be used effectively on one food source, it could be hypothesized that diet may not exert sufficient selective pressure to affect the evolution of radular morphology. The same conclusion may be drawn if one type of radula is used for a variety of food items.

Diet and feeding habits have been linked with radular morphology by a number of authors. Nybakken (1970: 316) found that the morphology of the radular teeth of three *Conus* species corresponds with their preying on amphinomids, an unusual prey item for *Conus*. Wu (1965b:102) has attributed the unique radular morphology of *Drupella* to its specialized food: coral polyps. He also stated that "... radular patterns displayed by ... [*Drupa ricina* (figures 17–19) and *Morula granulata*] ... may possibly be associated with the feeding habits of each species" (1965a:226). Taylor (1976), in discussing variations in muricid radulae, suspected a correlation between morphology and diet, and indicated the need for further study. Fretter and Graham (1962:172) reported that radular morphology and diet are directly correlated in prosobranchs.

On many occasions authors have suggested a cause and effect relationship between diet and radular morphology. The mechanisms by which this occurs are never mentioned directly, but natural selection is implicitly understood as the process by which diet may affect radular morphology. Solem (1974a:170) stated: "Evolutionary changes in the patterns of cusp and support structure are obviously one of the prime ways in which snails specialize within local areas or exploit different levels of food resources." Powell (1964:230) in discussing similar radular patterns in several turrid subfamilies says that a change in turrid radulae has taken place "... no doubt as a direct response to predaceous feeding." Marshall (1978:54) pointed out that radular specialization occurs in *Cerithiopsis*, in response to different structural and textural attributes of its prey.

Several authors have discussed convergence in radular

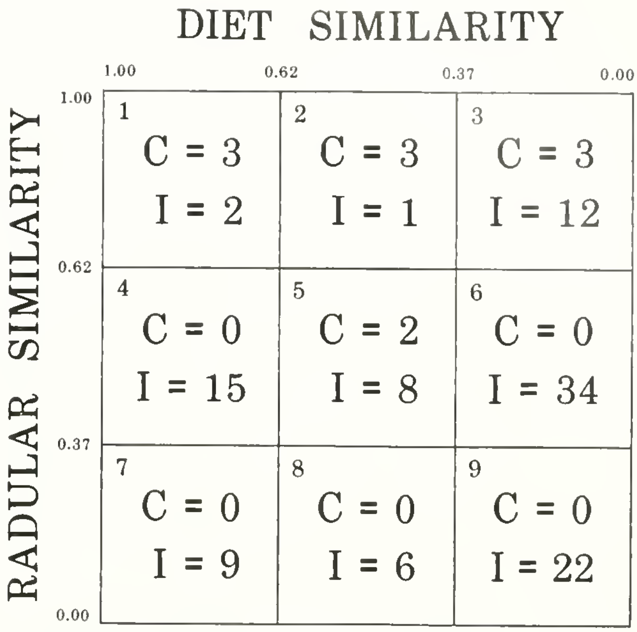

Figure 54. Distribution pattern of pairwise comparisons of thaidid taxa on the basis of similarities in diets and radulae. Number in upper left corner of each block denotes cell number C = pairs of congeners; I = pairs of intergeneric species.

morphology and seem to attribute this to diet. Houbrick (1975:15, 1978:15) stated convergence as the reason for not giving much weight to radular characters in his studies on the Cerithiacea. Convergence in radular morphology has also been discussed for Toxoglossa (Powell, 1964:230), herbivorous landsnails (Solem, 1973; Breure & Gittenberger, 1982), and for Muricacea (Harasewych, 1984:24).

Quantification of different relationships between radular morphology and diet, and quantification of convergence or parallelism in radular morphology becomes possible by dividing all pairwise combinations into different categories. The distribution of congeneric and intergeneric species pairs (figure 54) can be analyzed and the possible role of diet in causing convergence addressed. Parallelism is herein considered part of convergence. A clear discussion on the difference between parallel evolution and convergence is given in Gosliner and Ghiselin (1984:258).

Examples from Cell 1 suggest several possible explanations for radular similarity. Ancestral radular morphology may have been conserved, as evolutionary change in radular morphology is under phylogenetic constraint, or convergence has occurred. The similarity in the radulae of the three *Nucella* species is most likely due to common descent; all three species feed on shelled mollusks (primarily mussels) and barnacles. It is unnecessary to invoke diet as the external selective agent for a radular morphology especially useful for these prey items. Moreover, five other species, with different radular morphologies, have the same diet (see figure 53).

Convergence may explain similarity in radulae be-

tween intergeneric species found in Cell 1 (two pairs). And because dietary similarity is high between these taxa, diet could be invoked as the cause of these possible cases of convergence. Examples from other cells, however, suggest that this is at best a rare occurrence.

In Cell 3 there are more than three times as many species pairs with high radular similarity and low dietary similarity than species with high similarity for both, as in Cell 1. It is also noteworthy that the number of pairs between intergeners is six times higher in Cell 3 than in Cell 1, which shows that if the radular similarity in intergeners in Cell 3 were due to convergence, diet can be ruled out as a selective agent, since diets are not similar (*e.g.*, *Drupella cornus*, a coral feeder, and *Vexilla vexillum*, an urchin feeder). Therefore, high similarity in radular morphology is likely to be indicative of close phylogenetic affinities (conservation of radular characters), or is at most due to convergence not driven by diet.

The homogeneous, horizontal distribution of congeners (Cells 1–3, figure 54) shows that radular morphology is conserved, despite differences in dietary habits, and confutes diet as the selective force on divergence in radular morphology. The low number of pairs of intergeners in Cell 1 suggests that diet is not a strong selective force for convergence in radular morphology. Only if dissimilarity in radulae of congeners matches dietary dissimilarity, or if similarity in radulae of the intergeners matches dietary similarity (Cell 1), is searching for causes other than genealogical relationship necessary.

A comparison between Cells 1 and 7 shows that high dietary similarity corresponds more often with dissimilarity in radulae than with similarity in radulae. This applies to pairs of intergeners only, as radular similarity is consistently high between congeners, regardless of dietary similarity.

The high number of representatives in Cell 9 indicates that low radular similarity often corresponds with low dietary similarity. There is no need, however, to invoke diet to explain divergence in radular morphology amongst intergeners in this cell, because radular dissimilarity can be ascribed simply to general phylogenetic divergence.

Examination of individual cases of the 120 pairwise comparisons sheds light on why diet may not play an important role in the evolution of radular morphology. There are many examples showing that radulae of different morphologies are used for similar food items. This information is most easily derived from figure 53, which shows that mollusks are main food items for 11 of 16 species. Other examples suggest that similar radulae can be used for different food items. This occurs among species [*e.g.*, *Drupa rubusidaeus* (figures 20–22) and *Drupa morum*, *Vexilla vexillum* and *Drupella cornus*], and within species such as the "generalist" *Drupa ricinus*, which feeds on mollusks, small crustaceans, polychaetes, barnacles, sponges, and holothurians (figure 53; table 3).

The two pairs of congeners in Cell 5 indicate that although radular morphology may evolve at different rates among congeners, similarity in diet cannot be invoked as a cause.

The above findings suggest that radular characters are evolutionarily conservative in thaidid gastropods and dispel the need to invoke an adaptive scenario to explain radular morphology. If different radulae can be used for different food items, and if a similar (or one and the same) radula can be used for different food items, then radular morphology is not likely to be under high selective pressure from diet. If diet does not exert great selective pressure on radular morphology in any particular species, it cannot be the causal agent for convergence in radular morphology between those species.

It is possible that the highly unusual radular morphology of, for example, *Drupella cornus* is related to its food type (coral polyps). However, the radula of this species is very similar to that of *Vexilla vexillum*, which feeds on sea urchins. Further studies of diet and radular morphology of other species of *Drupella sensu stricto* and *Vexilla sensu stricto* will reveal if these unusual morphologies always correspond with the same diet. Perhaps other *Drupella* species with typical *Drupella* radulae feed on food items other than corals. I postulate that unique radular morphology is not necessarily the direct result of adaptation to a unique diet, but rather of relatively rapid accumulation of changes in the genome of the (ancestral) species. In such a case, the radula may be "pre-adapted" to coral feeding.

Although different taxa may have similar diets, feeding modes can differ substantially. Both *Drupella cornus* and coralliophilids, for example, feed on coral polyps (Robertson, 1970:49; Brawley & Adey, 1982), although coralliophilids lack radulae (Thiele, 1929:300; Robertson 1970:47). *Drupella* most likely scrapes the polyp, after liquifying it extracorporeally (Fankboner, 1970) whereas *Coralliophila* feeds suctorially (Ward, 1965:460). As more data on feeding modes become available, modes of feeding and application of the radula to the substrate may be added as a fourth variable, along with radular morphology, diet, and phylogenetic affinity. In order to detect correspondence between radulae and feeding modes, thaidids could then perhaps be divided into those that tear off large chunks of flesh, those that rasp off fine pieces of tissue, and those that bore through shells or barnacles prior to feeding. A similar categorization was used by Solem (1974b), who divided carnivorous land snails into "slicers", "stabbers", and those which slice and stab. Shimek and Kohn (1981) divided turrid radulae into six comparable functional groups.

Alterations in diet, due to changes in relative prey abundancy, are discussed for thaidids in West (1986) and Murdoch (1969). These examples of switching prey provide more evidence for the generalized function of thaidid radulae, and suggest that thaidid radular morphology has not evolved to accommodate any particular feeding mode or prey, and is not steered by adaptive processes.

Some of the radical changes in feeding modes or diets may correlate with a species' age and size. For example, juveniles of *Muricanthus nigritus* (Philippi, 1845) prey mainly upon barnacles, whereas adults prey mainly on gastropods (Paine, 1966:22). Brand and Lipps (1982) re-

ported that juveniles of the opisthobranch *Philene alata* prefer to feed on foraminifera, while adults prey upon small bivalves. Perhaps a smaller and narrower radula in a juvenile may be more suited for feeding on minute prey items than the adult radula with wider spaces between teeth cusps and denticles. It may thus be that spacing between different teeth, cusps, and denticles is of importance in food manipulation and food choice. Scaling should be taken into consideration in future studies of radular form and function to examine if distance between cusps and denticles influences food choice (or *vice versa*).

It may also be that ontogenetic (morphological) changes in radular morphology occur, which correspond with a switch in food items. Plaziat (1977:37) found such a correspondence in *Terebralia palustris* (Linné, 1767); juveniles of this species feed on micro-flora, but the adults eat only mangrove leaves. The radula in the adults is radically different from that in juveniles. However, no such ontogenetic changes combined with changes in dietary habits have been reported for thaidids.

More detailed studies on how radulae interact with prey substrate are essential to determine which teeth, cusps, and denticles are mostly involved in the actual scraping, slicing, or boring processes. Information on the mechanics of feeding may reveal if certain radular characters are more likely to be under dietary constraint than others; a topic which cannot be addressed at this time. It is possible that several different radular morphologies may be suitable for one food type if applied to the substrate differently. Hickman (1984) and Hickman and Morris (1985) have shown that the interplay (sequence and timing) between the different teeth in some archaeogastropods is rather complicated. In rachiglossates the possibilities of interaction are fewer because of a relatively simple tooth configuration (only one rachidian flanked on both sides by one lateral tooth).

In the Muricacea (and Naticidae), secretions of a boring organ aid in the mechanical penetration of prey prior to feeding (Carriker *et al.*, 1963; Carriker *et al.*, 1978; Carriker, 1981). These secretions facilitate penetration through $CaCO_3$ layers of shells and barnacles and may have similar effects on other outer body coverings in different prey. This may mean that a radula of general morphology is suitable for boring and feeding. Clearly, the interaction between the mechanical and biochemical manipulations in muricid feeding behaviour deserves more detailed attention.

Sexual dimorphism in radulae has been reported for several thaidid genera: *Nassa* Röding, 1798 (Maes, 1966), *Drupella* (Arakawa, 1957; Fujioka, 1982), *Morula* (Fujioka, 1984), and *Cronia* H. Adams & A. Adams, 1853 (Fujioka, 1984). No statements can be made on degree of sexual dimorphism in the species studied herein, because radulae were randomly dissected, in some cases, from only two individuals. Small differences, as reported in the literature for the above genera, would not substantially alter the character coding used here, and the results of this paper would not change. It would be interesting to assess diet of both sexes in species displaying sexual dimorphism. An identical diet for both sexes would present additional evidence of different radulae being suitable for one food type (Cell 7).

Another aspect that needs more detailed study is geographical variation in radular morphology and its possible correspondence with regional differences in prey availability. Dietary habits of individuals from different localities should be assessed, their radulae examined, and relationship between variation in diet and radular morphology studied. For example, Taylor (1983:308) found that *Drupa rubusidaeus* from Addu Atoll feeds mainly on demosponges, whereas specimens from other localities in the Indo-Pacific are polychaete-feeders. Conclusions drawn in this paper predict that the radulae of these populations are similar despite dietary differences.

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LITERATURE CITED

Abbott, R. T. 1974. American seashells, 2nd ed. Van Nostrand Reinhold Company, New York, 663 p., 24 pls.

Adams, H. and A. Adams. 1853. The genera of Recent Mollusca. John Van Voorst, London 1(1–8):1–256.

Arakawa, K. Y. 1957. On the remarkable sexual dimorphism of the radula of *Drupella*. Venus 19:52–58.

Arakawa, K. Y. 1962. A study on the radulae of the Japanese Muricidae. (1) The genera *Purpura*, *Thais* and *Mancinella*. Venus 22(1):70–78, pls. 5, 6.

Arakawa, K. Y. 1964. A study on the Japanese Muricidae. (2) The genera *Vexilla*, *Nassa*, *Rapana*, *Murex*, *Chicoreus* and *Homalocantha*. Venus 22(4):355–364, pl. 21.

Balaparameswara Rao, M. and P. V. Bhavanarayana. 1976. Environment and shell variation in relation to distribution of a tropical marine snail, *Drupa tuberculata* (Blainville). Journal of Molluscan Studies 42:235–242.

Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandelingen No. 214:188 p., 22 pls.

Bernstein, A. S. 1974. Diet and competition for food amongst predatory gastropods of limestone benches in Hawaii and Eniwetok. Ph.D. thesis, University of Oregon, Eugene, 147 p.

Brand, T. E. and J. H. Lipps. 1982. Foraminifera in the trophic structure of shallow-water Antarctic marine communities. Journal of Foraminiferal Research 12:96–104.

Brawley, S. H. and W. H. Adey. 1982. *Coralliophila abbreviata*: a significant corallivore! Bulletin of Marine Science 32(2):595–599.

Breure, A. S. H. and E. Gittenberger. 1982. The rock-scraping radula, a striking case of convergence (Mollusca). Netherlands Journal of Zoology 32(3):307–312.

Bruguière, J. G. 1789. Encyclopédie méthodique. Histoire naturelle des vers. Paris, 1(1):xvii + 344 p., pls. 287–488.

Butler, P. A. 1985. Synoptic review of the literature on the southern oyster drill *Thais haemastoma floridana*. NOAA Technical Report NMFS 35, 9 p.

Cake, E. W. 1983. Symbiotic associations involving the southern oyster drill *Thais haemastoma floridana* (Conrad) and macrocrustaceans in Mississippi waters. Journal of Shellfish Research 3(2):117–128.

Carriker, M. R. 1981. Shell penetration and feeding by naticean and muricacean predatory gastropods: a synthesis. Malacologia 20(2):403–422.

Carriker, M. R., D. B. Scott, and G. N. Martin. 1963. Demineralization mechanism of boring gastropods. *In:* Mechanisms of hard tissue destruction. American Association for the Advancement of Science, Publication No. 75, p. 55–89.

Carriker, M. R., L. G. Williams, and D. Van Zandt. 1978. Preliminary characterization of the secretion of the accessory boring organ of the shell-penetrating muricid gastropod *Urosalpinx cinerea*. Malacologia 17(1):125–142.

Cernohorsky, W. O. 1969. The Muricidae of Fiji—part II. Subfamily Thaidinae. The Veliger 11:293–315, pls. 47–49.

Cernohorsky, W. O. 1982. The taxonomy of some Indo-Pacific Mollusca. Part 10. Records of the Auckland Institute and Museum 19:125–147.

Cernohorsky, W. O. 1983. The taxonomy of some Indo-Pacific Mollusca. Part 11. Records of the Auckland Institute and Museum 20:185–202.

Clench, W. J. 1947. The genera *Purpura* and *Thais* in the western Atlantic. Johnsonia 2(23):61–75.

Colton, H. S. 1922. Variation in the dog whelk, *Thais* (*Purpura* auct.) *lapillus*. Ecology 3(2):146–157.

Connell, J. H. 1961. Effects of competition, predation by *Thais lapillus* and other factors on natural populations of the barnacle *Balanus balanoides*. Ecological Monographs 31:61–104.

Connell, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predator species of *Thais*. Ecological Monographs 40:49–78.

Conrad, T. A. 1837. Descriptions of new marine shells, from upper California. Collected by Thomas Nuttall, Esq. Journal of the Philadelphia Academy of Natural Sciences 7: 227–268.

Cooke, A. H. 1919. The radula in *Thais*, *Drupa*, *Morula*, *Concholepas*, *Cronia*, *Iopas*, and the allied genera. Proceedings of the Malacological Society of London 13(3–4): 90–110.

Cossmann, A. E. M. 1903. Essais de paléoconchologie comparée, Vol. 5. Paris, 215 p.

Crothers, J. H. 1983. Variation in dog-whelk shells in relation to wave action and crab predation. Biological Journal of the Linnean Society 20:85–102.

Crothers, J. H. 1985. Dog-whelks: an introduction to the biology of *Nucella lapillus*. Field Studies 6:291–360.

Demond, J. 1957. Micronesian reef-associated gastropods. Pacific Science 11:275–341, 4 pls.

Deshayes, G. P. 1839. Travaux inédits. Revue Zoologique par la Société Cuverienne 2:259–260, 356–361.

Duclos, M. 1832. Description de quelques espèces de pourpres servant de type a six sections établies dans ce genre. Annales des Sciences Naturelles 26:1–11, 2 pls.

Emerson, W. K. and W. O. Cernohorsky. 1973. The genus *Drupa* in the Indo-Pacific. Indo-Pacific Mollusca 3(13):1–40.

Emlen, J. M. 1966. Time, energy and risk in two species of carnivorous gastropods. Ph.D. thesis, University of Washington, Seattle, 138 p.

Fankboner, P. V. 1970. Notes on feeding and the functional morphology of the gut in the reef dwelling muricid *Morula elata* Blainville. The biology of molluscs. Hawaii Institute of Marine Biology, University of Hawaii, Technical Report No. 18, p. 6.

Fretter, V. and A. Graham. 1962. British prosobranch molluscs. Ray Society, London, 755 p.

Fujioka, Y. 1982. On the secondary sexual characters found in the dimorphic radula of *Drupella* (Gastropoda: Muricidae) with reference to its taxonomic revision. Venus 40: 203–223.

Fujioka, Y. 1984. Sexually dimorphic radulae in *Cronia margariticola* and *Morula musiva* (Gastropoda: Muricidae). Venus 43:315–330.

Fujioka, Y. 1985. Systematic evaluation of radular characters in Thaidinae (Gastropoda: Muricidae). Journal of Science of the Hiroshima University, Ser. B, Div. 1 (Zoology) 31(2): 235–287.

Gallardo, C. 1979. El ciclo vital del Muricidae *Concholepas concholepas* y consideraciones sobre sus primeras fases de vida en el bentos. Biologia Pesquera Chile 12:79–89.

Gmelin, J. F. 1791. In Linnaeus' Systema naturae, Tom. I, Pare VI, p. 3021–3909.

Golikov, A. N. and Y. I. Starobogatov. 1975. Systematics of prosobranch gastropods. Malacologia 15(1):185–232.

Gosliner, T. M. and M. T. Ghiselin. 1984. Parallel evolution in opisthobranch gastropods and its implications for phylogenetic methodology. Systematic Zoology 33(3):255–274.

Gunter, G. 1979. Studies of the southern oyster borer, *Thais haemastoma*. Gulf Research Reports 6(3):249–260.

Harasewych, M. G. 1984. Comparative anatomy of four prim-

itive muricacean gastropods: implications for trophonine phylogeny. American Malacological Bulletin 3(1):11–26.
Hickman, C. S. 1984. Implications of radular tooth-row functional integration for archaeogastropod systematics. Malacologia 25:143–160.
Hickman, C. S. and T. E. Morris. 1985. Gastropod feeding tracks as a source of data in analysis of the functional morphology of radulae. The Veliger 27(4):357–365.
Houbrick, R. S. 1975. Preliminary revision of supraspecific taxa in the Cerithiinae Fleming, 1822 (Cerithiidae: Prosobranchia). Bulletin of the American Malacological Union, Inc., p. 14–18.
Houbrick, R. S. 1978. The family Cerithiidae in the Indo-Pacific. Part 1: The genera *Rhinoclavis, Pseudovertagus, Longicerithium* and *Clavocerithium*. Monographs of Marine Mollusca No. 1, 130 p., 98 pls.
Hoxmark, R. C. 1971. Shell variation of *Nucella lapillus* in relation to environmental and genetic factors. Norwegian Journal of Zoology 19:145–148.
Jousseaume, F. 1888. Descriptions des mollusques recueilles par M. le Dr. Faurot dans la Mer Rouge et du Golfe d'Aden. Mémoires de la Société zoologique de France 1(2):12–223.
Kay, E. A. 1971. The littoral molluscs of Fanning Island. Pacific Science 25:260–281.
Kay, E. A. 1979. Hawaiian marine shells. Bishop Museum Press, Honolulu, 652 p.
Keen, A. M. 1971a. A review of the Muricacea. The Echo 4: 35.
Keen, A. M. 1971b. Sea shells of tropical West America. Stanford, 1064 p., 22 pls.
Kitching, J. A. and J. Lockwood. 1974. Observations on shell form and its ecological significance in thaisid gastropods of the genus *Lepsiella* in New Zealand. Marine Biology 28:131–144.
Kool, S. P. 1986a. Systematic revision of thaidid genera based on anatomy. American Malacological Bulletin 4(1):110.
Kool, S. P. 1986b. Radular convergence due to diet: an overestimated phenomenon? American Malacological Bulletin 4(2):233.
Kool, S. P. 1986c. Comparative anatomy of thaidid gastropods. Ninth International Malacological Congress, Edinburgh, Scotland, p. 43.
Lamarck, J. B. 1801. Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres des ces animaux. Paris, 432 p.
Largen, M. J. 1967. The diet of the dog-whelk, *Nucella lapillus* (Gastropoda Prosobranchia). Journal of Zoology 151: 123–127.
Linné, C. 1758. Systema naturae, 10th ed. Stockholm, 824 p.
Linné, C. 1767. Vermes Testacea. *In:* Systema naturae, 12th ed. 1(2):1106–1269.
Maes, V. O. 1966. Sexual dimorphism in the radula of the muricid genus *Nassa*. The Nautilus 79:73–80.
Marshall, B. A. 1978. Cerithiopsidae (Mollusca: Gastropoda) of New Zealand, and a provisional classification of the family. New Zealand Journal of Zoology 5:47–120.
Menge, B. A. 1978. Predation intensity in a rocky intertidal community. Oecologia 34:1–16.
Menke, K. T. 1828. Synopsis methodica molluscorum generum omnium et speciarum earum quae in Museo Menkeana adservabitur . . . . Pyrmont, i–xxi + 91 p.
Miller, A. C. 1970. Observations on the distribution and feeding of *Morula uva* (Bolten) and *Morula granulata* (Duclos) (Gastropoda: Thaisidae) in Hawaii. The biology of mollusks. University of Hawaii, Hawaii Institute of Marine Biology, Technical Report No. 18, p. 17.
Moore, H. B. 1936. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. Journal of the Marine Biological Association of the U.K. 21:61–89.
Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecological Monographs 39:335–354.
Nybakken, J. 1970. Correlation of radula tooth structure and food habits of three vermivorous species of *Conus*. The Veliger 12(1):316–318, 1 pl.
Paine, R. T. 1966. Function of labial spines, composition of diet, and size of certain marine gastropods. The Veliger 9(1):17–24.
Philippi, R. A. 1845. Abbildungen und Beschreibungen neuer oder weniger gekannter Conchilien (*Murex*). p. 191–192, 1 pl.
Plaziat, J. C. 1977. Les Cérithidés tropicaux et leur polymorphisme lie à l'écologie littorale des mangroves. Malacologia 16(1):35–44.
Ponder, W. F. 1973. The origin and evolution of the Neogastropoda. Malacologia 12(2):295–338.
Powell, W. B. 1964. The family Turridae in the Indo-Pacific. Indo-Pacific Mollusca 1(5):227–346.
Radwin, G. E. and A. D'Attilio. 1971. Muricacean supraspecific taxonomy based on the shell and the radula. The Echo 4:55–67.
Radwin, G. E. and A. D'Attilio. 1972. The systematics of some new world muricid species (Mollusca, Gastropoda), with descriptions of two new genera and two new species. Proceedings of the Biological Society of Washington 85: 323–352.
Radwin, G. E. and A. D'Attilio. 1976. *Murex* shells of the world. Stanford University Press, Stanford, 284 p.
Radwin, G. E. and H. W. Wells. 1968. Comparative radular morphology and feeding habits of muricid gastropods from the Gulf of Mexico. Bulletin of Marine Science 18:72–85.
Rafinesque, C. S. 1815. Analyses de la nature ou tableau du univèrs et des corps organisés. Barravecchia, Palermo, p. 5–6, 136–149, 218–223.
Reeve, L. 1846. Conchologia iconica. Vol. III. Monographs of the genera *Purpura, Ricinula* and *Monoceros*, 23 pls.
Robertson, R. 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. Pacific Science 24(1):43–54.
Röding, P. F. 1798. Museum Boltenianum. Hamburg, Part 1, p. 1–156, 4 pls.; Part 2, p. i–viii + 1–199.
Schumacher, C. F. 1817. Essay d'un nouveau système des habitations des vers testacés. Copenhagen, 287 p., 22 pls.
Shimek, R. L. and A. J. Kohn. 1981. Functional morphology and evolution of the toxoglossan radula. Malacologia 20(2): 423–438.
Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, 312 p.
Sneath, P. H. and R. R. Sokal. 1973. Numerical taxonomy. Freeman, San Francisco, 573 p.
Solem, G. A. 1973. Convergence in pulmonate radulae. The Veliger 15(3):165–171.
Solem, G. A. 1974a. The shell makers. Introducing mollusks. John Wiley and Sons, New York, 289 p.
Solem, G. A. 1974b. Patterns of radular tooth structure in carnivorous land snails. The Veliger 17(2):81–88.
Sowerby, G. B. 1834. Conchological illustrations, Part II. *Murex*—a catalogue of recent species. 9 p., pls. 58–67, 187–199.

Spight, T. M. 1976. Colors and patterns of an intertidal snail, *Thais lamellosa*. Researches on Population Ecology 17(2): 176–190.

Spight, T. M. 1979. Environment and life history: the case of two marine snails. The Belle W. Baruch Library in Marine Science No. 9, p. 135–143.

Spight, T. M. 1982. Population sizes of two marine snails with a changing food supply. Journal of Experimental Marine Biology and Ecology 57:195–217.

St. Amant, L. S. 1938. Studies on the distribution of the Louisiana oyster drill, *Thais floridana haysae* Clench. Thesis, Louisiana State University, 108 p.

Suchanek, T. H. 1978. The ecology of *Mytilus edulis* L. in exposed rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 31:105–120.

Suter, H. 1913. Manual of the New Zealand Mollusca. Wellington, New Zealand, 1120 p.

Swainson, W. A. 1840. Treatise on malacology or shells and shell-fish. London, 419 p.

Taylor, J. D. 1968. Coral reef and associated invertebrate communities (mainly molluscan) around Mahé, Seychelles. Philosophical Transactions of the Royal Society of London (B) 254:129–206.

Taylor, J. D. 1971. Reef associated molluscan assemblages in the Western Indian Ocean. Zoological Society of London, Symposium No. 28, p. 501–534.

Taylor, J. D. 1976. Habitats, abundance and diet of muricacean gastropods at Aldabra Atoll. Zoological Journal of the Linnean Society 59:155–193.

Taylor, J. D. 1978. Habitats and diet of predatory gastropods at Addu Atoll, Maldives. Journal of Experimental Marine Biology and Ecology 31:83–103.

Taylor, J. D. 1983. The food of coral-reef *Drupa* (Gastropoda). Zoological Journal of the Linnean Society 78:299–316.

Taylor, J. D. 1984. A partial food web involving predatory gastropods on a Pacific fringing reef. Journal of Experimental Marine Biology and Ecology 74:273–290.

Thiele, J. 1925. Gastropoda der deutschen Tiefsee-Expedition. Berlin, 382 p., pls. 13–46.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde, Part 1. Jena, 376 p.

Thomas, F. I. M. and A. J. Kohn. 1985. Trophic roles of the tropical limpet-like predatory gastropod, *Drupa*. American Zoologist 25(4):88.

Troschel, F. H. 1856–93. Das Gebiss der Schnecken zur Begründung einer natürlichen Classification, Vol. 2. Berlin, 409 p., 32 pls.

Vermeij, G. J. 1979. The architectural geography of some gastropods. *In:* Gray, J. and A. J. Boucot. Historical biogeography, plate tectonics, and the changing environment. Oregon State University Press, Corvallis, p. 428–433.

Vermeij, G. J. and J. D. Currey. 1980. Geographical variation in the strength of thaidid snail shells. Biological Bulletin 158:383–389.

Ward, J. 1965. The digestive tract and its relation to feeding habits in the stenoglossan prosobranch *Coralliophila abbreviata*. Canadian Journal of Zoology 43:447–464.

Wenz, W. 1941. Prosobranchia. *In:* Schindewolf. Handbuch der Palaeozoologie, Band 6, Teil 5, p. 961–1200.

West, L. 1986. Interindividual variation in prey selection by the snail *Nucella* (=*Thais*) *emarginata*. Ecology 67(3): 798–809.

Wilkinson, L. 1986. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, IL, 519 p.

Wu, S. K. 1965a. Comparative functional studies of the digestive system of the muricid gastropods *Drupa ricina* and *Morula granulata*. Malacologia 3(2):211–233.

Wu, S. K. 1965b. Studies of the radulae of Taiwan muricid gastropods. Bulletin of the Institute of Zoology, Academia Sinica 4:95–106.

Wu, S. K. 1968. On some radulae of the muricid gastropods. Venus 27(3):89–94, pl. 4.

Wu, S. K. 1973. Comparative studies on the digestive and reproductive systems of some muricid gastropods. Bulletin of the American Malacological Union, Inc., p. 18 (abstract).

Wu, S. K. 1985. The genus *Acanthina* (Gastropoda: Muricacea) in West America. Special Publications of the Mukaishima Marine Biological Station, p. 45–66.

Phreatodrobia coronae, a New Species of Cavesnail from Southwestern Texas

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ABSTRACT

Phreatodrobia coronae new species, a blind and unpigmented cavesnail, was collected from spring orifices at two sites in or near Del Rio, Val Verde County, Texas. This new species is separable from other known congeners by its free and largely uncoiled apex and has affinities with similar-shelled forms occurring in Balcones Fault Zone and Hill Country to the east.

INTRODUCTION

Edwards limestone and associated aquifers in southwestern Texas support a large phreatic fauna of about 50 species (Longley, 1981; Hershler and Longley, 1986a). Subterranean aquatic conditions in the region vary from air-exposed to deep artesian, with habitat size ranging from interstitial pores in limestone matrix to large solution caverns. Structural complexity of this phreatic system has facilitated differentiation of taxa, with the most speciose elements consisting of amphipod crustaceans (Holsinger and Longley, 1980, and references cited therein) and cavesnails of the family Hydrobiidae, comprising seven species of *Phreatodrobia* Hershler and Longley, 1986a, as well as three monotypic genera (Hershler and Longley, 1986a,b).

Fieldwork by the senior author during 1984 included collection of phreatic organisms from two springs in vicinity of Del Rio, Val Verde County (figures 1–3). Among the diverse fauna discovered was a highly distinctive blind cavesnail that we describe herein as a new species of *Phreatodrobia*.

SYSTEMATICS

Phreatodrobia coronae Hershler new species
Del Rio cavesnail
(figures 4–21; table 1)

Materials examined: Holotype (figure 6; USNM 859219), a dry shell of 1.27 mm width, from unnamed spring on E side of Devils River in canyon just downflow from Slaughter Bend, Val Verde County, Texas, Satan Canyon (1972) 1: 24000, *ca.* 5.1 km NW of SE corner of quadrangle, elevation *ca.* 342 m, R. Hershler and S. Corona, 17 IX 1984. Additional series from type locality include 7 (dry shells) paratypes (USNM 859154, collected by S. Corona, 26 VIII 1986), and a lot split into dried (10) and alcohol (13) specimens (USNM 859156, collected by S. Corona, 1–8 IX 1986). Single series (USNM 859164; 13 empty shells and 2 alcohol specimens) also from small spring (San Felipe Springs) on W side of San Felipe Creek by #2 hole on San Felipe Country Club N of HW 90 in Del Rio, Val Verde, Texas, Del Rio SW (1972) 1: 24000, *ca.* 1.1 km SW of NE corner of quadrangle, elevation *ca.* 290 m, R. Hershler, 14 IX 1984.

Diagnosis: A small-sized species with near-planispiral to low-trochoid shell having loosely coiled, protruding apex. Teleoconch sculpture consisting of 10–20 collabral varices or costae and 30–40 strong spiral lines. Opercular peg well-developed. Ctenidium absent. Central tooth of radula with single pair of basal cusps. Intestinal coil in pallial roof complex.

Description: Shell measurements and counts for 7 paratypes (sexes mixed) are in table 1. Shell (figures 4–13) transparent, colorless, about a millimeter wide with 3 tubular, moderately expanding whorls. Protoconch whorls, 1.25. Periostracum light brown. Sutures deeply impressed. Translation rate (and therefore shell height) variable (ranging from *ca.* 1.0 to 2.0), yielding diversity in shell form (figures 6–9). First ¼ whorl of protoconch (figure 10) free and nearly uncoiled, producing horn-like apex strongly contrasting with teleoconch shape. Aperture *ca.* 30–40° oblique to coiling axis with adapical portion extended forward, near-circular in cross section, moderately flared all around, often slightly fluted above and below. Inner lip well-thickened and either separate from or narrowly adnate to body whorl above. Umbilicus broadly open (figure 5). Protoconch with wrinkled pits (figures 4, 12, 13). Strong spiral lines beginning at end of protoconch, with costae beginning 0.5–1.0 whorl later. Lines are uniformly spaced all around exposed portions of whorls and cross collabral sculpture (figure 11). The

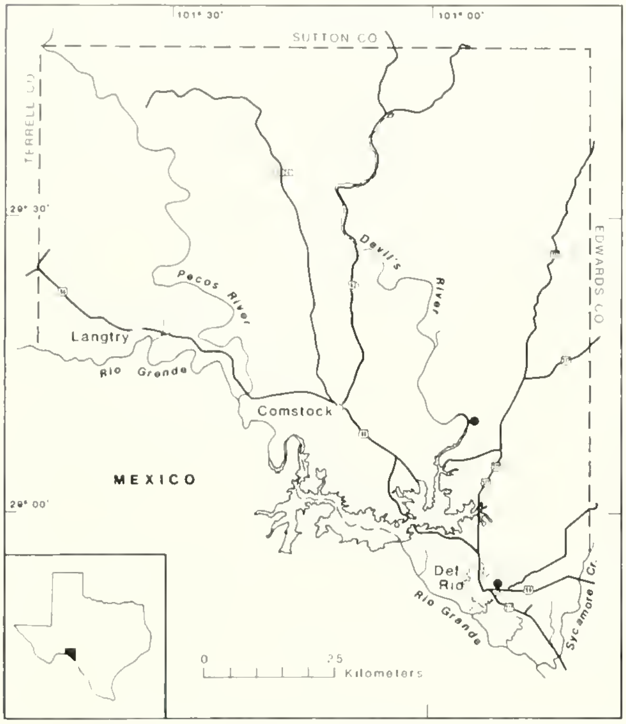

Figure 1. Map of Val Verde County, Texas, showing drainage and collecting sites (filled circles). Adapted from General Highway Map, Val Verde County, Texas.

latter varying from low varices to lamelliform costae, typically slightly curved forward.

Operculum (figures 14–16) amber, paucispiral, near-circular, with 4 whorls and strong peg located sub-centrally on inner (ventral) surface. Operculum and peg corneous. Peg height several times thickness of remaining operculum (figure 16). Pedal attachment scar elliptical.

Radular formula (from figures 17–20): centrals, 6(7)-1-(7)6/1-1; laterals, 5-1-6; inner marginals, 17-18; outer marginals, 18. Central teeth (figure 17) broadly trapezoidal. Cusps on all teeth elongate, often dagger-like.

Animal without eyespots and melanic pigment. Scattered black (internal) granules on dorsal stomach and ventral style sac.

Pallial cavity longer than wide, with majority of roof occupied by intestine (In, figure 21). Osphradium (Os) small, positioned anterior to pallial intestine near mantle collar.

Stomach slightly longer than style sac. Pallial intestine looping twice, with first loop inside of second; long axes of loops parallel to pallial cavity length (figure 21). Anus located along columellar edge near mantle collar.

Testis (Ts, figure 21) a simple sac filling much of digestive gland posterior to stomach. Seminal vesicle (Sv) con-

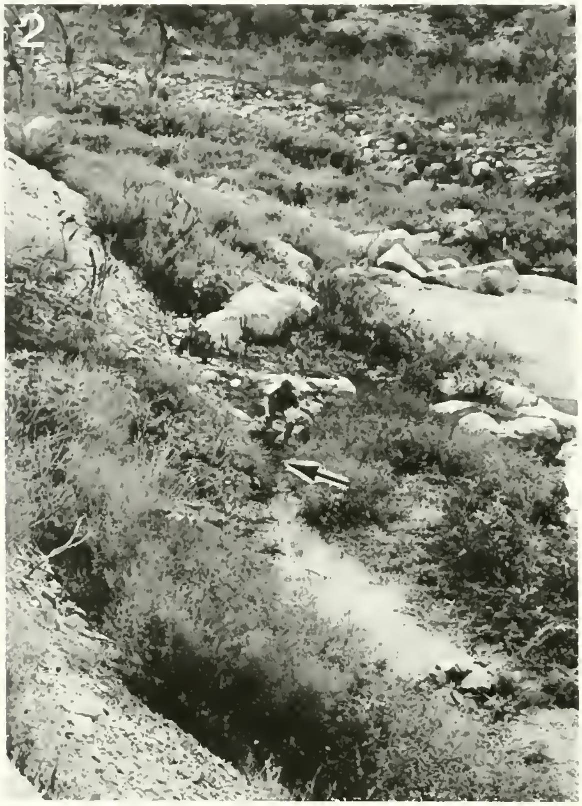

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Figure 2. Photograph (8 IX 1986) of collecting site at unnamed spring on E side of Devils River just downflow from Slaughter Bend, Val Verde County, Texas. Arrow indicates location of spring source. **Figure 3.** Photograph (8 IX 1986) of collecting site at San Felipe Springs on W side of San Felipe Creek on San Felipe Country Club, Del Rio, Val Verde County, Texas. Arrow indicates location of spring source.

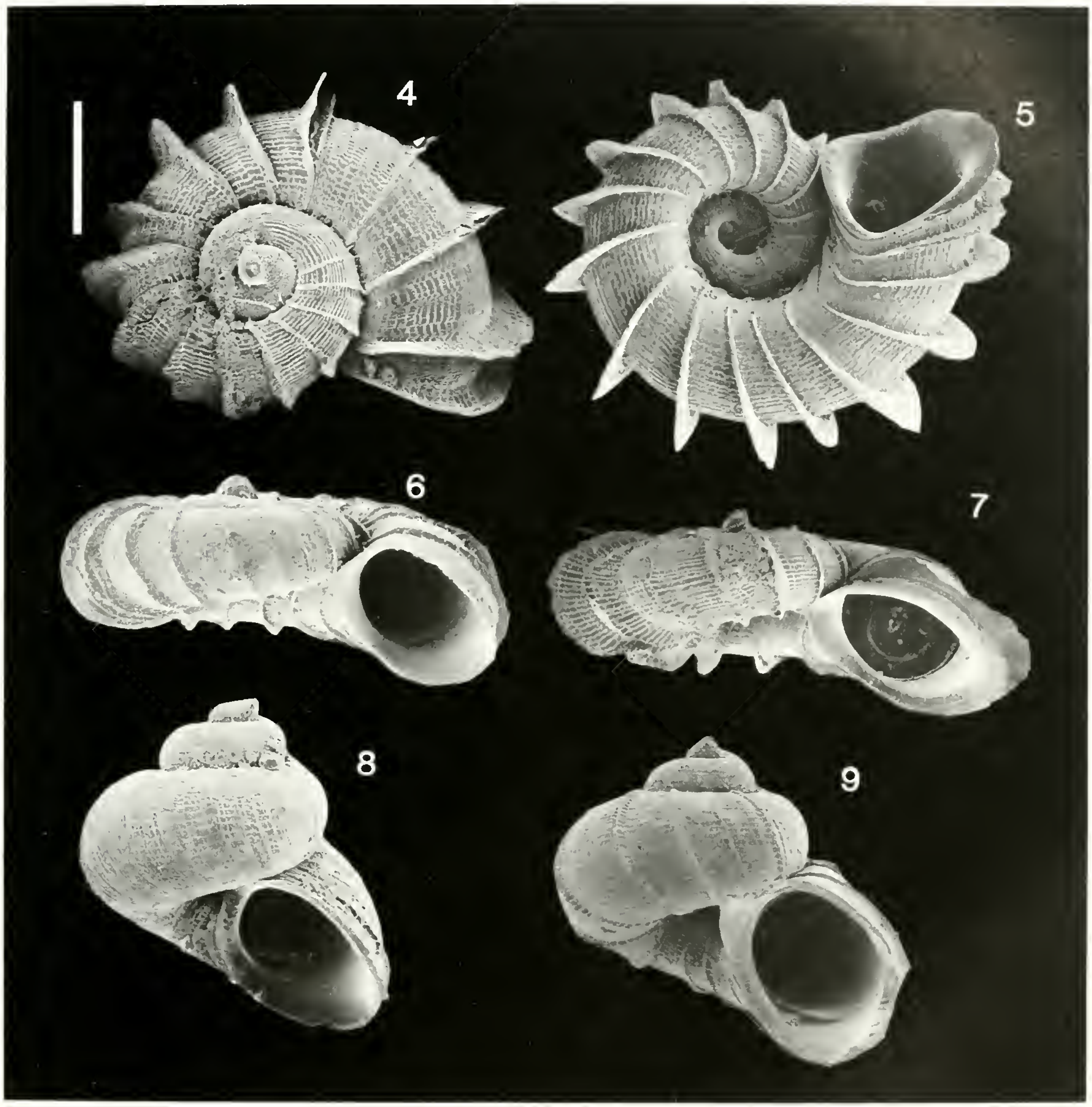

Figure 4. Photograph (SEM) of apical shell aspect of *Phreatodrobia coronae* new species from unnamed spring on E side of Devils River just downflow from Slaughter Bend, Val Verde County, Texas. Scale bar = 0.5 mm. **Figure 5.** Photograph (SEM) of umbilical shell aspect of *P. coronae*. Locality and scale as above. **Figure 6.** Photograph (SEM) of holotype of *P. coronae* new species. Locality and scale as above. **Figure 7.** Photograph (SEM) of shell of *P. coronae* new species. Locality and scale as above. **Figure 8.** Photograph (SEM) of shell of *P. coronae* from San Felipe Springs, Del Rio, Val Verde County, Texas. Scale as above. **Figure 9.** Photograph (SEM) of shell of *P. coronae*. Locality as above. Scale as above.

sisting of a few thickened coils anterior to testis and abutting against prostate gland. Vas efferens absent. Prostate gland (Pr) yellow-colored, elongate (twice as long as wide), almost totally posterior to pallial cavity. Posterior vas deferens entering near posterior tip of gland; anterior vas deferens (Vd2) exiting from anterior tip and travelling straight path in pallial cavity floor. Penis (not figured) simple, coiling on right side of "neck." Filament *ca.* ⅓ penis length, tapering distally. Vas deferens without undulations in penis.

Description of female anatomy limited due to lack of sufficient material. Ovary a white-colored, simple sac

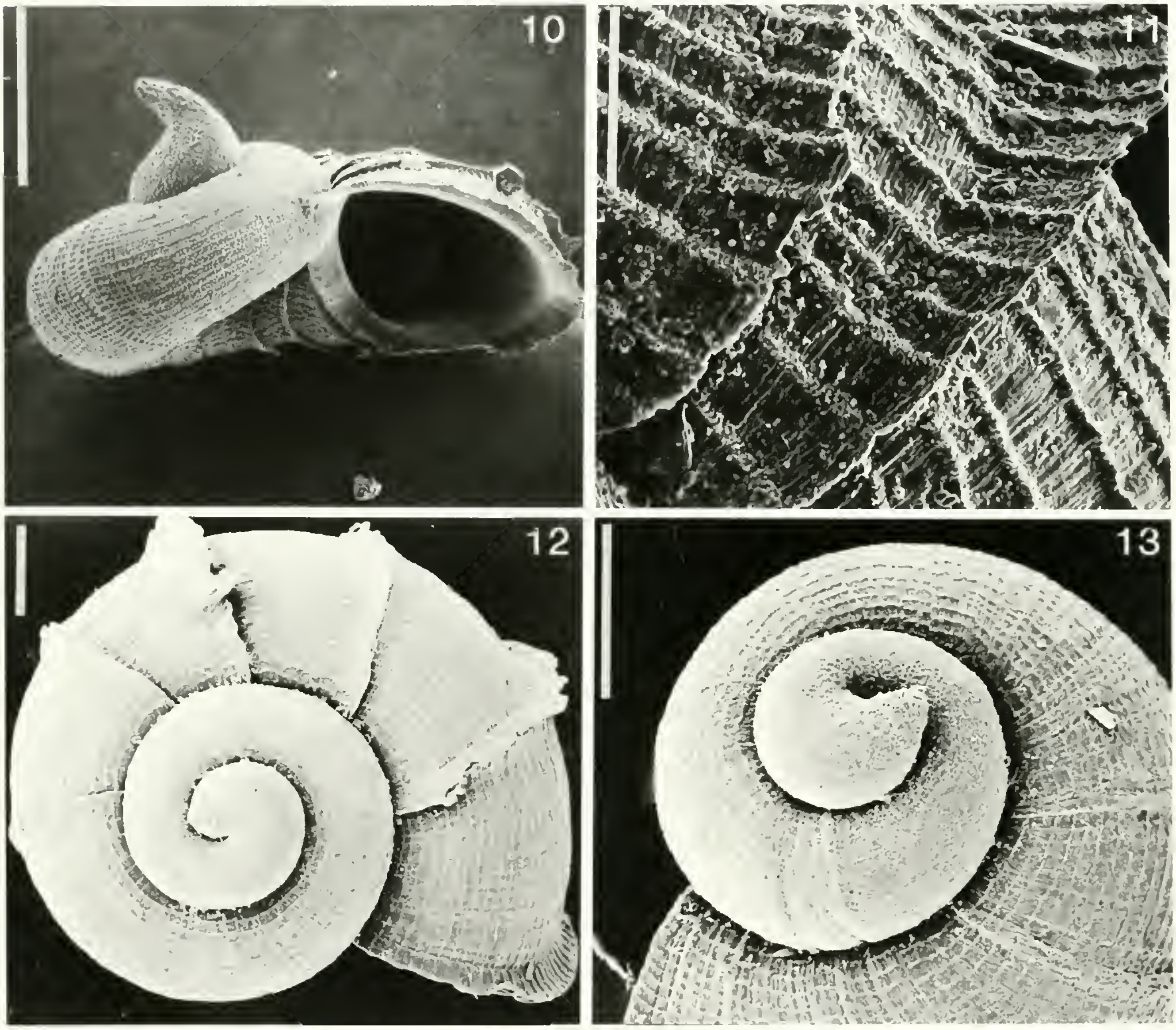

Figure 10. Photograph (SEM) of juvenile shell of *P. coronae* from unnamed spring on E side of Devils River just below Slaughter Bend, Val Verde County, Texas. Scale bar = 240 μm. **Figure 11.** Photograph (SEM) showing teleoconch sculpture of *P. coronae*. Locality as above. Scale bar = 23 μm. **Figure 12.** Photograph (SEM) of apical shell aspect of *P. coronae* from San Felipe Springs, Del Rio, Val Verde County, Texas. Scale bar = 150 μm. **Figure 13.** Photograph (SEM) showing shell apex of *P. coronae*. Locality as above. Scale bar = 200 μm.

filling *ca.* 20% of body length. Anterior end of pallial oviduct simple, with broad, slit-like, terminal opening. Bursa copulatrix largely posterior to albumen gland. Seminal receptacle not seen; sperm storage perhaps occurring in single, highly swollen oviduct coil located just proximal to opening into albumen gland.

Variation: Differentiation among the two known populations is evident, as shells from spring on Devils River vary from near-planispiral to low-trochoid (shell height/width, 45–85%) and typically have well-developed and numerous collabral costae, whereas examples from San Felipe Springs are usually low-trochoid (shell height/width, 80–100%), with collabral sculpture weakly developed (figures 6–9 show extremes of shell form). It is clear that shell form and sculpture pattern overlap in these populations and we therefore choose to consider them as a single species.

Etymology: Named in honor of Mrs. Susannah J. Corona and family for their assistance in obtaining material of this species from the type locality.

Comparisons: *Phreatodrobia coronae* is separable from all other congeners by its unique protoconch. While resembling *P. imitata* Hershler and Longley, 1986a, in

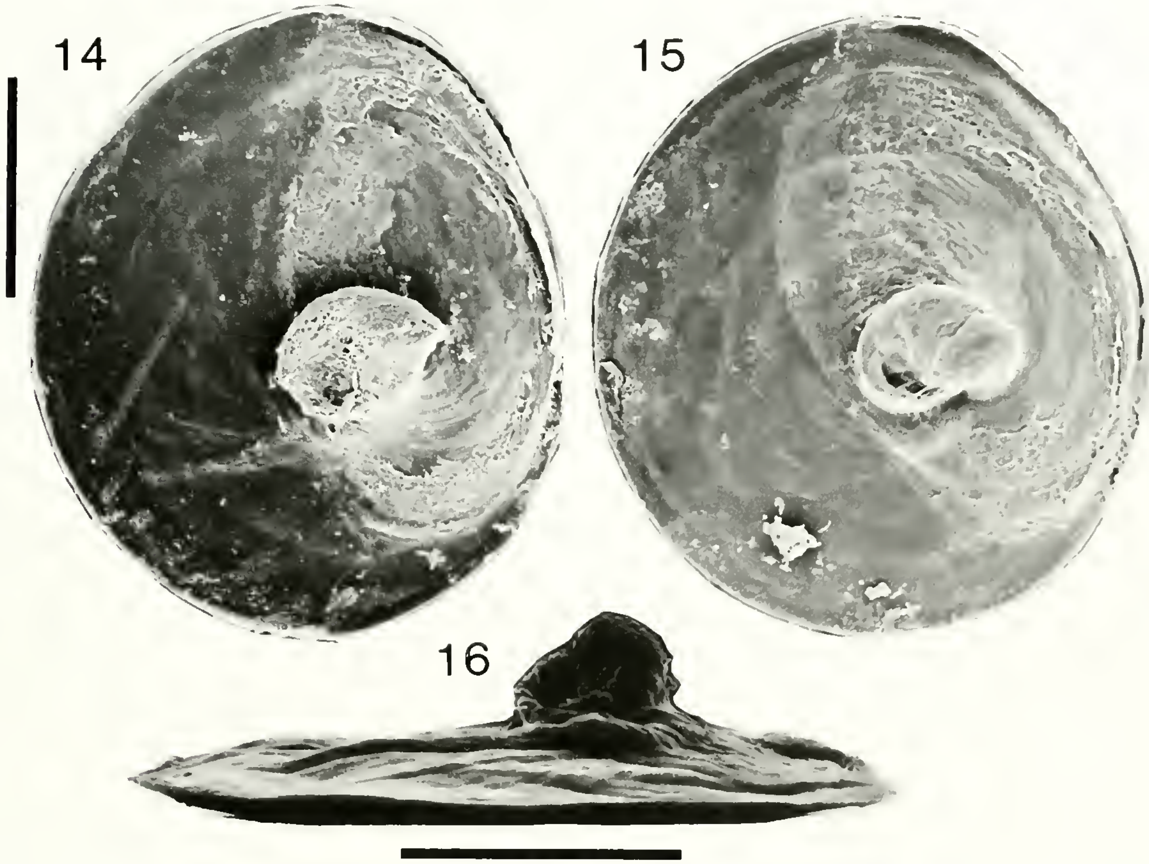

Figure 14. Photograph (SEM) of ventral aspect of operculum (showing peg and muscle attachment scar) of *P. coronae* from unnamed spring on E side of Devils River just below Slaughter Bend, Val Verde County, Texas. Scale bar = 150 μm. **Figure 15.** Photograph (SEM) of ventral aspect of operculum of *P. coronae*. Locality and scale as above. **Figure 16.** Photograph (SEM) of lateral aspect of operculum (showing height of peg) of *P. coronae*. Locality as above. Scale bar = 150 μm.

terms of teleoconch sculpture pattern, *P. coronae* is clearly allied to *P. nugax* (Pilsbry and Ferriss, 1906) and *P. micra* (Pilsbry and Ferriss, 1906) from Balcones Fault Zone and Hill Country (to the east) on basis of simple, near-planispiral to low-trochoid shells and similarities in radular and female reproductive morphology (see Hershler & Longley, 1986a). The novelty described herein is distinguished from both of the above by well-developed teleoconch sculpture (collabral costae known from single population of *P. nugax*; Hershler & Longley, 1986a: fig. 4U), complex pallial intestine, and absence of gill filaments; and further separable from *P. nugax* by smaller size and more highly developed opercular peg.

Discussion: Both sites (figures 2, 3; latter also shown in Brune, 1975: fig. 6) are moderate-sized rheocrenes having single, discrete orifices that were netted (for method, see Hershler & Longley, 1986a:130–131) to collect phreatic biota. Nets could not be tightly fitted into the rather large orifice at San Felipe Springs and small size of resulting samples is probably due to sweeping of specimens out of net or feeding by fishes. With current decreased flow of Goodenough and Comal Springs, San Felipe Springs, collectively discharging *ca.* 70–100 feet^3/sec, now rank as second largest in the state and may be increasing due to local recharge from Amistad Reservoir (Brune, 1975). Water source for these springs is Georgetown limestone of Edwards Aquifer (Brune, 1975). The unnamed spring on Devils River is periodically sub-

Table 1. Measurements (mm) and counts from seven shells (paratypes) of *Phreatodrobia coronae* new species from unnamed spring on E side of Devils River just below Slaughter Bend, Val Verde County, Texas.

Character	Mean	Range	Standard deviation
Number of whorls	3.0	—	—
Shell height	0.67	0.53–0.81	0.09
Shell width	1.11	1.04–1.17	0.05
Body whorl length	0.55	0.42–0.66	0.08
Body whorl width	0.81	0.73–0.89	0.05
Aperture length/width	1.01	0.85–1.22	0.13
Number of collabral varices	16.71	14.0–21.0	2.7

Figure 17. Photograph (SEM) of central radular teeth of *P. coronae* from unnamed spring on E side of Devils River just below Slaughter Bend. Scale bar = 3.8 μm. **Figure 18.** Photograph (SEM) of lateral (above) and inner marginal (below) radular teeth of *P. coronae*. Locality as above. Scale bar = 2.7 μm. **Figure 19.** Photograph (SEM) of lateral (3) and inner marginal (2) radular teeth of *P. coronae*. Locality as above. Scale bar = 3.8 μm. **Figure 20.** Photograph (SEM) of outer marginal radular tooth of *P. coronae*. Locality as above. Scale bar = 1.76 μm.

merged when Amistad Reservoir crests above conservation level (340.4 m). Discharge of this spring is *ca.* 2–4 feet^3/sec and water source is likely the same as that for nearby Slaughter Bend springs: Georgetown limestone (Brune, 1975).

Collections from San Felipe Springs included an additional undescribed cavesnail belonging to Hydrobiidae: Littoridininae and having affinities with *Balconorbis* Hershler and Longley, 1986a, from Uvalde County. This was also collected from the unnamed spring on Devils River as were blind and unpigmented amphipod crustaceans, asellid and cirolanid isopods, and copepods. Included among the amphipods are forms having affinities with taxa from Comal, Kendall, and Hays counties to the east (J. R. Holsinger, letter to senior author dated 13 IX 1986).

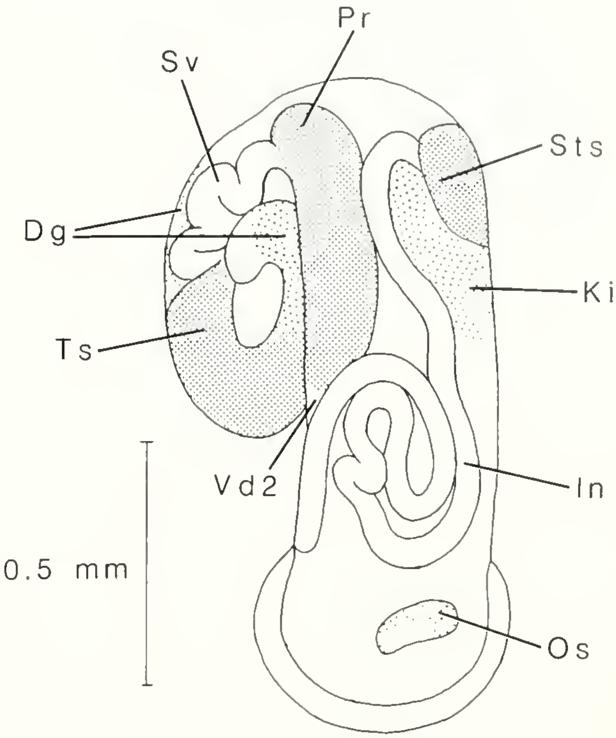

Figure 21. Dorsal aspect (minus head foot) of male *P. coronae* from unnamed spring on E side of Devils River just below Slaughter Bend, Val Verde County, Texas. Dg = digestive gland; In = intestine; Ki = kidney; Os = osphradium; Pr = prostate; Sts = style sac; Sv = seminal vesicle; Ts = testis; Vd2 = anterior vas deferens.

ACKNOWLEDGEMENTS

We thank the National Park Service at Amistad National Recreation Area (especially staff at Rough Canyon) and San Felipe Country Club for permission to sample springs. The former also provided transportation to collecting sites on several occasions. The study could not have been completed without the field assistance of Mrs. S. Corona. Fieldwork of the senior author was partly funded by United States Fish and Wildlife Service (Contract No. 14-16-0002-84-228, Amendment No. 1).

LITERATURE CITED

Brune, G. 1975. Major and historical springs of Texas. Texas Water Development Board Report 189:94 p.

Hershler, R. and G. Longley. 1986a. Phreatic hydrobiids (Gastropoda: Prosobranchia) from the Edwards (Balcones Fault Zone) Aquifer region, south-central Texas. Malacologia 27: 127–172.

Hershler, R. and G. Longley. 1986b. *Hadoceras taylori*, a new genus and species of phreatic Hydrobiidae (Gastropoda: Rissoacea) from south-central Texas. Proceedings of the Biological Society of Washington 99:121–136.

Holsinger, J. R. and G. Longley. 1980. The subterranean amphipod crustacean fauna of an artesian well in Texas. Smithsonian Contributions to Zoology 308:62 p.

Longley, G. 1981. The Edwards Aquifer: earth's most diverse groundwater ecosystem? International Journal of Speleology 11:123–128.

Morphological Anomalies in the Shell of Natural Populations of *Helisoma trivolvis* Say (Gastropoda: Planorbidae)

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ABSTRACT

A total of 157 natural populations of *Helisoma trivolvis* Say in central and western North America were examined for the occurrence of whorl deflection. The anomaly was observed significantly more frequently than expected due to chance in ponds, on fine bottom sediments, and in waters with low dissolved organic matter and low combined nitrate and nitrite concentrations. Certain habitat characteristics may enhance the occurrence of this anomaly, but it is not known whether genetic factors or ecologically induced effects are responsible.

INTRODUCTION

Recently Gomez et al. (1986) reported the incidence of varying frequencies of phenotypic anomalies in a number of natural populations of *Biomphalaria glabrata* Say, 1818 in the Dominican Republic. The deformity most frequently observed consisted of whorl deflection and overlapping, resulting in shells that were not entirely planispiral. Genetic factors were strongly suspected as the responsible agents.

The present paper reports the incidence of a similar anomaly in natural populations of another planorbid, *Helisoma trivolvis* Say, 1816 (nomenclature according to Clarke, 1981), an ultrasinistral species. Distribution of the occurrence of the anomaly was studied in central and western North America with respect to type of water body, type of bottom substrate, eight water chemistry parameters, and plant and snail species richness of the communities in which the planorbids were found.

MATERIALS AND METHODS

Living and freshly dead individuals of *H. trivolvis* were examined at 157 sites located in British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, North Dakota, and Minnesota. All sites contained water year-round. Most sites were visited once during 1972–85.

A surface water sample was collected at 127 sites, placed on ice and frozen within a maximum of 48 hr after collection. Total dissolved solids, total alkalinity, chloride, sulphate, molybdenum reactive phosphorus (MRP), combined nitrate and nitrite, and dissolved organic matter (DOM) were determined using methods recommended by the American Public Health Association (1971). The pH was determined directly in the field using a portable pH meter. Ten of the sites were sampled a number of different times; for these, extreme water chemistry values were used for statistical analysis.

Species richness of gastropod and macrophyte communities was assessed during a search time of 1 hr at each site, by wading or by dredging with a rake from a small boat.

In statistical analyses, sites at which the anomaly was present were compared with those at which it appeared to be absent (henceforth designated as found and remaining sites, respectively). Frequency values of the incidence within individual populations were not used because of the widely varying numbers of individuals that could be obtained for examination at the different sites. Values of $p < 0.05$ were considered significant for all statistical tests.

RESULTS

The most frequently observed anomaly in *H. trivolvis* consisted of deflection of the whorl away from the plane of coiling, accompanied by uneven partial overlap onto the preceding whorl (figures 1–4). In some specimens deflections were repeated a number of times during growth. The incidence of deflection at various sites ranged from 0 to 100% of the shells examined. The anomaly was observed at 44 of the 157 sites investigated (28%), and was seen in all regions of the study area, indicating that it was quite widespread. However it appeared to be noticeably more frequent west of the Precambrian Shield boundary.

Types of water bodies were classified as ponds (< 10 ha), lakes (> 10 ha), rivers (> 2 m deep), and creeks (< 2 m deep). The frequencies of the water body types were compared for found and remaining sites using 2×4 chi-square tests. The results indicated a significant difference in overall distribution (chi-square = 10.3, $p = 0.016$,

df = 3). Ponds showed the greatest proportion of found to remaining sites (0.71, N = 60), followed by combined lotic habitats (0.22, N = 22) and lakes (0.18, N = 45). Student-Newman-Keuls multiple comparison tests indicated that the difference between ponds and all other water body types was significant.

Bottom substrate was classified according to the predominant type at each site. Frequencies of substrate types were compared at found and remaining sites using chi-square tests. Overall differences were marginally significant (chi-square = 13.7, p = 0.05, df = 7). Sand and clay showed the highest proportions of found to remaining sites (0.75, N = 28, and 0.61, N = 37, respectively), followed by silt (0.50, N = 12), highly organic sediments (0.33, N = 16), and gravel (0.04, N = 24). Samples were too small for shale, limestone, and granitic bedrock for adequate comparison. The Student-Newman-Keuls procedure indicated that incidence of the anomaly was significantly lower on gravel than on either sand or clay; other differences were not significant.

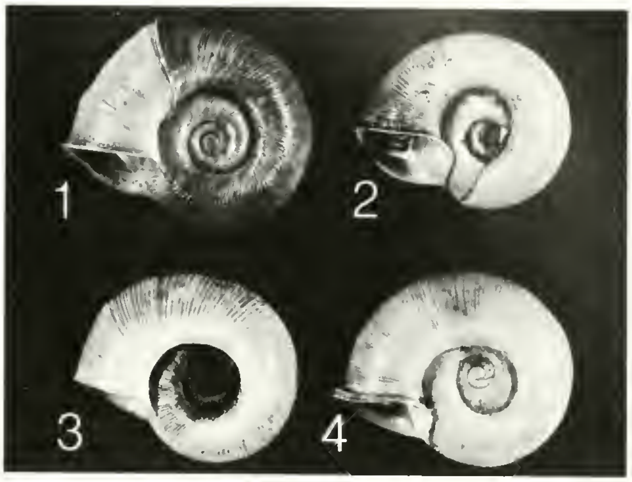
Water chemistry was examined at found and remaining sites using unpaired t-tests, provided that the results of F-tests were not significant; otherwise nonparametric comparisons were made using Kolmogorov-Smirnov two-sample tests. Mean values were higher at found than at remaining sites for total dissolved solids, total alkalinity, chloride, and MRP (table 1), but these differences were not significant because of the variability of the values in both groups. Thus, while the mean value of chloride was almost 10 times greater at found than at remaining sites, the degree of overlap between the two groups rendered this difference insignificant. However, combined nitrate and nitrite, and DOM showed significantly lower mean values at found than at remaining sites.

Species richness at found and at remaining sites was not significantly different for macrophyte communities (Kolmogorov-Smirnov Z = 0.77, p = 0.60) or for gastropod communities (t = 0.42, p = 0.68).

DISCUSSION

Whorl deflection and open coiling has been noted in other planorbid genera (Meier-Brook, 1983), as well as in *H. trivolvis* and related species (Baker, 1936, 1945). In the present study whorl deflection was encountered in populations found over the entire geographic area studied, but was relatively infrequent in eastern Manitoba, Ontario, and Minnesota. The anomaly was most often encountered where DOM and combined nitrate and nitrite values were comparatively low; other inorganic parameters (except sulphate and pH) were also somewhat higher at many, but not all, sites where the abnormality was present. These characteristics (except low nitrate-nitrite) coincided with areas west of the Precambrian Shield boundary. However, this abnormality was correspondingly rare where waters with higher DOM and lower inorganic values did occur west of the Shield.

While Gomez et al. (1986) noted that deformed *Biomphalaria glabrata* were often associated with excessive calcareous deposits on the shell, in the present study such differences were not evident between normal and deformed shells of *H. trivolvis* within the same population.



Figures 1–4. Upper views of normal (1) and abnormal (2–4) specimens of *Helisoma trivolvis*. **1.** Marsh ditch, Delta Marsh, Lake Manitoba, Manitoba (25.5 mm). **2.** Pond, 9.6 km east of Richer, Manitoba (22.0 mm). **3.** Pembina River at Hwy. No. 34, Manitoba (22.5 mm). **4.** First Vermilion Lake, near Banff, Alberta (24.0 mm).

Table 1. Mean water chemistry values at sites where deformed shells were and were not observed. Values of t or Kolmogorov-Smirnov Z are given as appropriate.

Parameter	Normal			Deformed			Significance
	$\bar{x}$	SE	N	$\bar{x}$	SE	N	
pH	8.1	0.1	97	8.1	0.2	40	t = 0.11, p = 0.92
Total dissolved solids, mg/liter	372	58	94	395	65	40	Z = 1.00, p = 0.27
Total alkalinity, mg/liter $CaCO_3$	143	11	96	176	17	40	t = 1.66, p = 0.10
Chloride, mg/liter	8	2	95	71	25	38	Z = 0.96, p = 0.32
Sulphate, mg/liter	38	6	96	39	12	40	Z = 0.50, p = 0.97
Combined nitrate and nitrite, mg/liter	1.37	0.11	96	0.94	0.12	40	Z = 1.43, p = 0.03*
Molybdenum reactive phosphorus, mg/liter	3.18	0.34	96	4.03	0.75	40	Z = 0.85, p = 0.46
Dissolved organic matter, absorbance (acidified) at 275 nm	0.35	0.02	95	0.22	0.02	34	Z = 1.77, p = 0.004*

* Significant difference.

However deformed shells were usually present in thick-shelled populations; anomalous individuals were seldom seen in calcium-poor, DOM-rich Shield waters, where shells were thin and contained a high proportion of organic material.

The significant tendency for the deformity to occur in ponds may have been associated with the more extreme conditions that are often encountered in small water bodies, for example higher inorganic concentrations, greater seasonal environmental fluctuations in water chemistry and temperature, and elevated infection rates by various pathogenic organisms. Finer sediments were also significantly more frequently associated with this anomaly than were coarser materials, perhaps as a result of the greater frequency of fine sediments in quiet ponds.

If genetic factors contribute towards the anomaly in *H. trivolvis*, the higher frquencies of this anomaly in ponds may be associated with a greater likelihood of self-fertilization (*e.g.*, Meier-Brook, 1983) and inbreeding in small, genetically limited populations. It is also possible that gene expression or penetrance may be modified or enhanced by particular environmental factors. If genetic factors are not involved, it may be an ecologically induced effect. Other factors, such as infection with parasites, pollution, thermal stress, etc. cannot be ruled out, since these are also more likely to be pronounced in small water bodies. Clearly much additional study is required.

LITERATURE CITED

American Public Health Association. 1971 Standard methods for the examination of water and wastewater. American Public Health Association. New York, 874 p.

Baker, F. C. 1936. The freshwater mollusc *Helisoma corpulentum* and its relatives in Canada National Museum of Canada Bulletin No. 79:1–33.

Baker, F. C. 1945. The molluscan family Planorbidae. University of Illinois Press, Urbana, IL, 519 p.

Clarke, A. H 1981. The freshwater molluscs of Canada. National Museums of Canada, Ottawa, 446 p.

Gomez, J., M. Vargas, and E. A Malek. 1986. Morphological anomalies in the shell of field-collected *Biomphalaria glabrata* (Say, 1818). The Nautilus 100:53–55

Meier-Brook, C. 1983. Taxonomic studies on *Gyraulus* (Gastropoda—Planorbidae). Malacologia 24:1–113.

Prehistoric Freshwater Mussel Assemblages of the Mississippi River in Southwestern Wisconsin

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ABSTRACT

Archaeological excavations at aboriginal sites adjacent to the Upper Mississippi River (UMR) in southwestern Wisconsin produced a series of freshwater mussel (naiad) assemblages that contained more than 29,000 valves of 28 mussel species. These subfossil mussel valves are the remains of mollusks harvested as a food source by prehistoric peoples between circa A.D. 1 and A.D. 1000. Taken together, the aboriginal assemblages provide an approximation of the regions' main stem UMR naiad communities during the latter part of the prehistoric era. A quantitative comparison of the subfossil collection with modern mussel survey data documents dramatic changes in the species composition of molluscan communities following habitat degradation of the UMR associated with EuroAmerican settlement.

INTRODUCTION

The navigation pools of the present-day Upper Mississippi River (UMR) were created by a series of locks and dams built by the U.S. Army Corps of Engineers during the 1930's and 1940's (Rasmussen, 1979:4). Although a number of recent studies have focused on freshwater mussels (naiades) in the UMR (*e.g.*, Havlik & Stansbery, 1978; Mathiak, 1979; Perry, 1979, Fuller, 1980; Thiel, 1981; Duncan & Thiel, 1983; Havlik, 1983), there are few pre-lock and dam, taxon specific reports of naiad distribution prior to significant habitat modification and the large scale commercial harvest that severely depleted mussel populations during the late 19th and early 20th century.

Some early reports on UMR freshwater mussels (Pratt, 1876; Witter, 1883; Marsh, 1887; Shimek, 1888) offer information on the presence and relative abundance of particular species, but lack quantitative data. Later studies undertaken by the U.S. Bureau of Fisheries and others during the period of intense mussel harvest for the pearl button industry (Smith, 1899; Baker, 1905; Coker, 1919; Coker *et al.*, 1921) provided detailed information on specific taxa, but lacked quantitative data on entire mussel assemblages. The survey by Ellis in 1930–31 (Van der Schalie & Van der Schalie, 1950) provided the only quantified pre-lock and dam information on mussels encompassing a large portion of the main stem UMR. This survey evaluated mussel resources after several decades of unregulated harvest to supply shell for the button industry (Baker, 1903; Coker, 1919:66–69; Knott, 1980: 11–16) and regional outbreaks of 'pearl fever' when portions of the UMR were depleted of mussels in search of salable pearls (Kunz, 1898:395; Baker, 1905:250–251). Moreover, the UMR of Ellis' survey had undergone significant habitat changes due to construction of a hydroelectric dam at Keokuk, Iowa (Coker, 1914), modification of channel dynamics as a result of hundreds of wing and closing dams (Grier, 1926:92; Rasmussen, 1979:3–4), and heavy siltation (Ellis, 1936). The results of the Ellis survey reflect a stage in the degradation of the UMR, and are not representative of naiad communities prior to EuroAmerican settlement.

In 1978–80, archaeological excavations were conducted by personnel from the University of Wisconsin–Madison at a number of Woodland Tradition (A.D. 1 to A.D. 1000) prehistoric Indian habitation sites adjacent to the UMR in southwestern Wisconsin. Several of these sites contained food refuse deposits (middens) of freshwater mussel shells, each accurately dated by the radiocarbon method and/or through associated artifactual remains of known age. In the following report, nine prehistoric mussel assemblages are described. Eight of these subfossil assemblages from six sites were excavated during 1978–80 near the city of Prairie du Chien, adjacent to present-day Pool 10, in Crawford County, Wisconsin, and one assemblage was excavated in 1956 by David A. Baerreis at a site located in the Pool 11 area of Grant County, Wisconsin (see figure 1 and table 1). A detailed description of archaeological information for each site is presented in Theler (1983).

METHODS AND MATERIALS

The mussel remains excavated during the 1978–80 fieldwork were bagged with their surrounding matrix and returned to the Department of Anthropology, University of Wisconsin–Madison. At the department's Laboratory of Archaeology, shells were cleaned, identified, and placed into storage. The mussel assemblage collected by Baerreis in 1956 is housed at the Laboratory of Archaeology, where it was studied by the author in 1981. A series of

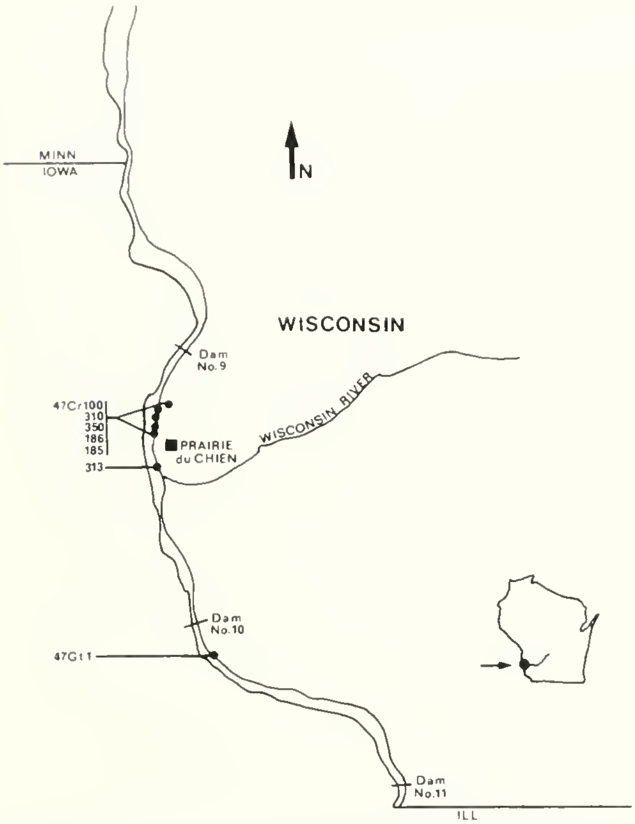

Figure 1. The location of described prehistoric shell middens in Pools 10 and 11 of the Upper Mississippi River.

voucher specimens for each of the taxa in the prehistoric assemblages is on deposit at the Ohio State University, Museum of Zoology (OSUM). The taxonomic nomenclature used in this report follows that presented by Stansbery (1982) and employed by Oesch (1984). The use of certain subspecific designations for subfossil material in this report is in keeping with the catalogued voucher series at OSUM.

RESULTS

The nine subfossil mussel assemblages from the navigational Pools 10 and 11 areas of UMR have a combined total of 29,198 valves, representing 13,384 individuals that could be identified as belonging to one of 28 species. The species represented, number of valves, minimum number of individuals (MNI), and the relative abundance (%) are presented for each assemblage in table 2. The MNI were determined by the maximum number of right or left valves of each species in each assemblage. These assemblages are combined in table 3 to facilitate comparisons with the historic surveys of Ellis (Van der Schalie & Van der Schalie, 1950), Thiel (1981) and Duncan and Thiel (1983). The quality of shell preservation varies between sites and is indicated to some degree by the number of unidentifiable valves listed for each assemblage (table 2). These valves were specifically unidentifiable due to damage or deterioration in virtually all cases.

The most abundant mussel species in the UMR subfossil material was the ebony shell, *Fusconaia ebena* (Lea, 1831) represented by 7,794 individuals comprising 58.23% of the combined assemblages. One of the most common UMR mussel species during the late 19th century, *F. ebena* occurred on a substrate of sand and/or gravel under a moderate to strong current velocity (Marsh, 1887: 47; Smith, 1899:290, 298; Coker, 1914:8, 1919:20, 22; Parmalee, 1967:31). The second most frequently encountered taxon was the monkey face mussel, *Quadrula metanevra* (Rafinesque, 1820) with 1,033 individuals totaling 7.72% of the prehistoric assemblages. *Q. metanerva* is reported to have occurred with the ebony shell in a similar habitat setting (Coker, 1919:42).

Fusconaia ebena and *Q. metanevra* together total 65.95% of the UMR subfossil fauna with only eight of the remaining 26 species contributing more than 1.0% each. These eight are *Amblema plicata* (Say, 1817), with 920 individuals representing 6.87% of the combined assemblages, *Pleurobema sintoxia* (Rafinesque, 1820) 5.91%, *Quadrula pustulosa* (Lea, 1831) 4.56%, *Fusco-*

Table 1. UMR archaeological site locations.

Site number	Name	Location
47Cr350	Bullhead Slough Shell Midden	Mississippi River Mile (MRM) 639.0 adjacent to abandoned side channel trace, Bullhead Slough, in the SW ¼ of section 1, T7N, R7W, Crawford County, Wisconsin
47Cr310	Quarter Mile Shell Midden	MRM 638.9 adjacent to abandoned side channel trace, "Mud Slough" in SW ¼ of section 1, T7N, R7W, Crawford County, Wisconsin
47Cr100	Mill Coulee Shell Heap	At mouth of Mill Coulee, in the NE ¼, NW ¼ of section 6, T7N, R6W, Crawford County, Wisconsin
47Cr186	Mill Pond Site	MRM 636.9 adjacent to "Marais Lake" in the NW ¼, SW ¼ of section 13, T7N, R7W, Crawford County, Wisconsin: 47Cr186-1, Lower Shell Midden; 47Cr186-2, Upper Shell Midden; 47Cr186-3, refuse pit (Feature 26) filled with shell
47Cr185	Mill Run Site	MRM 636.2 adjacent to "Marais Lake" in the NE ¼, SE ¼ of section 23, T7N, R7W, Crawford County, Wisconsin
47Cr313	Hunter Channel Midden	MRM 632.3, on western shore of Schmidt Island, in the NW ¼ of section 12, T6N, R7W, Crawford County, Wisconsin
47Gt1	Stonefield Village	MRM 608.8 in section 13, T3N, R6W, Grant County, Wisconsin

naia flava (Rafinesque, 1820) 4.09%, *Actinonaias ligamentina carinata* (Barnes, 1823) 3.72%, *Obovaria olivaria* (Rafinesque, 1820) 2.56%, *Elliptio dilatata* (Rafinesque, 1820) 1.54%, and *Cyclonaias tuberculata* (Rafinesque, 1820) with 185 individuals representing 1.38% of the UMR subfossil material.

The remaining 18 species each contributed less than 1% to the prehistoric UMR assemblages and include in decreasing frequency of relative abundance, *Ellipsaria* (= *Plagiola*) *lineolata* (Rafinesque, 1820) with 83 individuals representing 0.62% of the combined subfossil material, *Plethobasus cyphyus* (Rafinesque, 1820), *Obliquaria reflexa* Rafinesque, 1820, *Quadrula quadrula* (Rafinesque, 1820), *Elliptio crassidens crassidens* (Lamarck, 1819), *Tritogonia verrucosa* (Rafinesque, 1820), *Truncilla truncata* Rafinesque, 1820, *Ligumia recta* (Lamarck, 1819), *Lampsilis higginsi* (Lea, 1857), *Quadrula nodulata* (Rafinesque, 1820), *Lampsilis ventricosa* (Barnes, 1823), *Lampsilis radiata luteola* (Lamarck, 1819) (= *L. r. siliquoidea* (Barnes, 1823)), *Potamilus alatus* (Say, 1817), *Lasmigona costata* (Rafinesque, 1820), *Lasmigona complanata* (Barnes, 1823), *Lampsilis teres teres* (Rafinesque, 1820), *Strophitus undulatus undulatus* (Say, 1817), and *Arcidens confragosus* (Say, 1829) with one individual and representing 0.01% of the UMR subfossil material.

DISCUSSION

The value of aboriginal shell deposits as a baseline to measure change in a stream's molluscan community since prehistoric times has been recognized by numerous researchers (*e.g.*, Morrison, 1942; Stansbery, 1965; Parmalee *et al.*, 1980, 1982; Taylor & Spurlock, 1982; Parmalee & Bogan, 1986). The mussels recovered from the UMR aboriginal shell middens are considered to be an indicator of naiad distribution and relative abundance prior to EuroAmerican disruption of the main stem UMR aquatic ecosystem.

In the UMR subfossil assemblages, the ebony shell, *F. ebena* was the most abundant species in eight of nine discrete midden deposits and contributed nearly 60% of all individuals represented. During the late 19th century, *F. ebena* occurred in the main stem UMR in dense aggregates or "beds" containing millions of individuals (Smith, 1899:299; Coker, 1919:22). Marsh (1887:43) stated that *F. ebena* "is the most abundant species in the [Mississippi] river, equalling in numbers all other species of Uniones combined." Coker (1919:20, 24) describes *F. ebena* as comprising 75 to 80% of (commercial) species at Le Claire, Pleasant Valley, and at other points above Davenport, Iowa. In species counts made by Coker at commercial shell piles north of Keokuk, Iowa in 1912, he found 80% were *F. ebena*, 10% *Q. metanevra*, while seven other species (unspecified by Coker) accounted for the remaining 10%. It would appear that *F. ebena* comprised a major component of the UMR naiad fauna for at least two millennium before overharvest for the button industry, siltation, and the impediment of this species' unique host fish (the skipjack herring, *Alosa chrysochloris*) with the construction of the hydroelectric dam at Keokuk, Iowa in 1913, spelled its demise in the UMR (Surber, 1913; Coker, 1914, 1930:165–169).

In modern surveys, *F. ebena* represented only 0.18% of Ellis' 1930–31 (Van der Schalie & Van der Schalie, 1950) survey efforts within the present-day Pool 10 area, while the recent work by Thiel (1981) and Duncan and Thiel (1983) failed to locate any living individuals. However, a small number of relict *F. ebena* were found living in Pool 10 near Prairie du Chien by Mathiak (1979) and more recently by David Heath (personal communication). *Quadrula metanevra* has also drastically declined relative to prehistoric numbers, with this species comprising 0.2% or less of the recent surveys in Pool 10 (see table 2).

The three ridge mussel, *Amblema plicata* contributes 6.87% of the combined subfossil assemblages, and accounted for more than 10.0% of an assemblage in only two instances (table 1). In the Ellis survey, *A. plicata* accounted for 7.46% of all species in the Pool 10 area region, while this taxon represented 72.1 and 52.9%, respectively, in systematic surveys by Thiel (1981) and Duncan and Thiel (1983). The three ridge mussel has become the most abundant UMR mussel species, thriving in the often turbid, reduced velocity waters of the present-day river.

Another species showing substantial population changes in the UMR is the washboard mussel, *Megalonaias nervosa* (Rafinesque, 1820). *Megalonaias nervosa* was not represented in the prehistoric material from Pools 10 and 11, but has been recovered in very small numbers with prehistoric UMR assemblages near Rock Island, Illinois (Van Dyke *et al.*, 1980). A single valve of this species was present at the Millville archaeological site (Theler, 1983) on the lower Wisconsin River 18 km above its junction with Pool 10 of the UMR. *Megalonaias nervosa* represented 1.33% of the Ellis survey in the Pool 10 area (Van der Schalie & Van der Schalie, 1950) and 2.8% and 6.8% of Thiel (1981) and Duncan and Thiel (1983) surveys, respectively, for Pool 10 (table 2). *Megalonaias nervosa*, like *A. plicata*, has shown a population increase under present-day habitat conditions.

A number of mussel species that appear to have maintained or slightly increased from their prehistoric population densities include *Quadrula pustulosa*, *Fusconaia flava*, *Elliptio dilatata*, and *Lampsilis higginsi*. Two species, *Elliptio c. crassidens* and *Cyclonaias tuberculata* were present in small numbers in all the prehistoric assemblages, but appear to be extirpated from the present-day main stem UMR. *Plethobasus cyphyus* and *Tritogonia verrucosa* occurred in small numbers in seven of the nine subfossil assemblages, while *Pleurobema sintoxia*, *Actinonaias ligamentina carinata*, and *Ellipsaria lineolata* occur in low to moderate numbers in all prehistoric assemblages. The four latter species have been reduced to small, relict populations and *P. cyphyus* is extirpated in the UMR Pools 10 and 11 region.

Havlik and Stansbery (1978:9) have documented ap-

Table 2. Freshwater mussels (Naiades) recovered from prehistoric shell middens in the Pool 10 and 11 area of the upper Mississippi River.

Site number: / Approximate date:	47Cr186-1 A.D. 70			47Cr313 A.D. 160			47GT1 A.D. 170–430			47Cr100 A.D. 280–330		
	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%
Family Unionidae												
Subfamily Anodontinae												
Strophitus u. undulatus (Say, 1817)	3	2	0.06	0	0	0.00	0	0	0.00	0	0	0.00
Arcidens confragosus (Say, 1829)	0	0	0.00	0	0	0.00	0	0	0.00	1	1	0.08
Lasmigona complanata (Barnes, 1823)	4	4	0.12	0	0	0.00	0	0	0.00	0	0	0.00
Lasmigona costata (Rafinesque, 1820)	6	4	0.12	0	0	0.00	0	0	0.00	0	0	0.00
Subfamily Ambleminae												
Tritogonia verrucosa (Rafinesque, 1820)	26	15	0.43	2	2	0.42	1	1	0.13	5	5	0.41
Quadrula quadrula (Rafinesque, 1820)	19	10	0.29	0	0	0.00	0	0	0.00	26	16	1.31
Quadrula metanevra (Rafinesque, 1820)	399	202	5.82	20	13	2.71	177	90	12.02	156	82	6.69
Quadrula nodulata (Rafinesque, 1820)	6	3	0.09	0	0	0.00	0	0	0.00	5	4	0.33
Quadrula pustulosa (Lea, 1831)	310	163	4.70	17	10	2.08	55	31	4.14	195	103	8.41
Amblema plicata (Say, 1817)	476	242	6.97	10	6	1.25	20	14	1.87	196	106	8.65
Fusconaia ebena (Lea, 1831)	3,253	1,700	48.99	573	312	65.00	987	510	68.09	1,157	608	49.63
Fusconaia flava (Rafinesque, 1820)	432	220	6.34	50	32	6.67	20	11	1.47	145	75	6.12
Cyclonaias tuberculata (Rafinesque, 1820)	45	23	0.66	23	15	3.13	23	14	1.87	3	3	0.24
Plethobasus cyphyus (Rafinesque, 1820)	36	20	0.58	0	0	0.00	16	10	1.34	7	4	0.33
Pleurobema sintoxia (Rafinesque, 1820)	438	224	6.46	69	38	7.92	47	24	3.20	200	106	8.65
Elliptio c. crassidens (Lamarck, 1819)	15	9	0.26	5	4	0.83	5	3	0.40	2	2	0.16
Elliptio dilatata (Rafinesque, 1820)	287	145	4.18	5	4	0.83	3	2	0.27	29	16	1.31
Subfamily Lampsilinae												
Obliquaria reflexa Rafinesque, 1820	27	17	0.49	8	7	1.46	3	2	0.27	21	13	1.06
Actinonaias ligamentina carinata (Barnes, 1823)	580	308	8.88	23	14	2.92	33	17	2.27	69	39	3.18
Ellipsaria lineolata (Rafinesque, 1820)	64	34	0.98	10	7	1.46	2	1	0.13	13	7	0.57
Obovaria olivaria (Rafinesque, 1820)	188	96	2.77	19	13	2.71	25	13	1.74	32	19	1.55
Truncilla truncata Rafinesque, 1820	2	2	0.06	2	2	0.42	0	0	0.00	6	3	0.24
Potamilus alatus (Say, 1817)	3	2	0.06	0	0	0.00	0	0	0.00	0	0	0.00
Ligumia recta (Lamarck, 1819)	8	5	0.14	0	0	0.00	0	0	0.00	8	6	0.49
Lampsilis teres teres (Rafinesque, 1820)	0	0	0.00	0	0	0.00	2	2	0.27	2	1	0.08
Lampsilis radiata luteola (Lamarck, 1819)	13	7	0.20	0	0	0.00	1	1	0.13	0	0	0.00
Lampsilis higginsi (Lea, 1857)	11	7	0.20	0	0	0.00	2	2	0.27	4	4	0.33
Lampsilis ventricosa (Barnes, 1823)	6	6	0.17	1	1	0.21	1	1	0.13	3	2	0.16
Subtotal	6,657	3,470	100.02	837	480	100.02	1,423	749	100.01	2,285	1,225	99.98
Unidentifiable valves	1,082	—	—	190	—	—	26	—	—	152	—	—
Totals	7,739	3,470	100.02	1,027	480	100.02	1,449	749	100.01	2,437	1,225	99.98

Table 2. Continued.

	47Cr186-2 A.D. 400–700			47Cr186-3 Pit Feature 26 A.D. 400–700			47Cr185 A.D. 700–1000			47Cr310 A.D. 800			47Cr350 A.D. 990		
	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%	Valves	MNI	%
Family Unionidae															
Subfamily Anodontinae															
Strophitus u. undulatus	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Arcidens confragosus	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Lasmigona complanata	0	0	0.00	0	0	0.00	2	1	0.07	0	0	0.00	0	0	0.00
Lasmigona costata	2	1	0.12	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Subfamily Ambleminae															
Tritogonia verrucosa	6	3	0.36	0	0	0.00	6	5	0.35	1	1	0.03	0	0	0.00
Quadrula quadrula	6	3	0.36	6	3	0.56	17	9	0.63	12	7	0.19	2	2	0.23
Quadrula metanevra	92	51	6.07	112	56	10.37	63	32	2.23	825	425	11.27	151	82	9.41
Quadrula nodulata	2	1	0.12	2	1	0.19	3	2	0.14	0	0	0.00	1	1	0.11
Quadrula pustulosa	50	28	3.33	91	47	8.70	79	50	3.48	170	94	2.49	150	84	9.64
Amblema plicata	428	217	25.83	27	16	2.96	610	306	21.28	10	6	0.16	10	7	0.80
Fusconaia ebena	354	188	22.38	611	306	56.67	1,487	787	54.73	5,575	2,826	74.94	1,056	557	63.95
Fusconaia flava	68	37	4.40	35	18	3.33	122	74	5.15	102	55	1.46	46	26	2.99
Cyclonaias tuberculata	16	8	0.95	25	13	2.41	17	12	0.83	141	77	2.04	37	20	2.30
Plethobasus cyphyus	3	3	0.36	0	0	0.00	12	6	0.43	38	24	0.64	15	11	1.26
Pleurobema sintoxia	383	196	23.33	86	45	8.33	157	80	5.56	113	65	1.72	24	13	1.49
Elliptio c. crassidens	7	4	0.48	1	1	0.19	17	9	0.63	3	3	0.08	2	2	0.23
Elliptio dilatata	51	28	3.33	1	1	0.19	13	7	0.49	2	2	0.05	1	1	0.11
Subfamily Lampsilinae															
Obliquaria reflexa	4	2	0.24	5	3	0.56	9	5	0.35	27	16	0.42	12	8	0.92
Actinonaias ligamentina carinata	97	49	5.83	23	12	2.22	40	22	1.53	49	29	0.77	11	9	1.03
Ellipsaria lineolata	26	13	1.55	10	5	0.93	7	5	0.35	10	6	0.16	7	5	0.57
Obovaria olivaria	9	5	0.60	15	8	1.48	39	20	1.39	246	128	3.40	72	40	4.59
Truncilla truncata	0	0	0.00	4	2	0.37	0	0	0.00	7	6	0.16	4	3	0.34
Potamilus alatus	3	2	0.24	0	0	0.00	6	3	0.21	0	0	0.00	0	0	0.00
Ligumia recta	0	0	0.00	3	2	0.37	3	2	0.14	0	0	0.00	0	0	0.00
Lampsilis teres teres	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00	0	0	0.00
Lampsilis radiata luteola	1	1	0.12	0	0	0.00	1	1	0.07	0	0	0.00	0	0	0.00
Lampsilis higginsi	0	0	0.00	2	1	0.19	0	0	0.00	0	0	0.00	0	0	0.00
Lampsilis ventricosa	0	0	0.00	0	0	0.00	0	0	0.00	1	1	0.03	0	0	0.00
Subtotal	1,608	840	100.00	1,059	540	100.02	2,710	1,438	100.04	7,332	3,771	100.01	1,601	871	99.97
Unidentifiable valves	542	—	—	—	—	—	880	—	—	446	—	—	358	—	—
Totals	2,150	840	100.00	1,069	540	100.02	3,590	1,438	100.04	7,778	3,771	100.01	1,959	871	99.97

Table 3. A comparison of some prehistoric and modern freshwater mussel (naiad) assemblages from the upper Mississippi River.

		Pool 10		
Data source:	This report; subfossil	Ellis, 1930–31	Thiel, 1981	Duncan and Thiel, 1983
Number of individuals:	13,384	1,126	4,516	12,150
	%	%	%	%
Family Unionidae				
Subfamily Anodontinae				
Anodonta imbecillis Say, 1829	0.00	0.89	<0.1	1.6
Anodonta suborbiculata Say, 1831	0.00	0.00	0.0	<0.1
Anodonta grandis subspp.	0.00	7.19	0.3	0.8
Strophitus undulatus undulatus (Say, 1817)	0.01	0.09	0.3	0.4
Arcidens confragosus (Say, 1829)	0.01	0.27	0.2	0.3
Simpsonaias ambigua (Say, 1825)	0.00	0.09	0.0	0.0
Lasmigona complanata (Barnes, 1823)	0.04	0.00	<0.1	0.1
Lasmigona costata (Rafinesque, 1820)	0.04	0.00	0.0	0.0
Subfamily Ambleminae				
Megalonaias nervosa (Rafinesque, 1820)	0.00	1.33	2.8	6.8
Tritogonia verrucosa (Rafinesque, 1820)	0.24	2.04	0.0	<0.1
Quadrula quadrula (Rafinesque, 1820)	0.37	0.09	3.1	1.8
Quadrula metanevra (Rafinesque, 1820)	7.72	0.09	0.2	0.1
Quadrula nodulata (Rafinesque, 1820)	0.09	0.71	3.2	0.9
Quadrula pustulosa (Lea, 1831)	4.56	2.93	6.7	3.5
Amblema plicata (Say, 1817)	6.87	7.46	72.1	52.9
Fusconaia ebena (Lea, 1831)	58.23	0.18	0.0	0.0
Fusconaia flava (Rafinesque, 1820)	4.09	1.24	5.9	3.5
Cyclonaias tuberculata (Rafinesque, 1820)	1.38	0.09	0.0	0.0
Plethobasus cyphyus (Rafinesque, 1820)	0.58	0.00	0.0	0.0
Pleurobema sintoxia (Rafinesque, 1820)	5.91	0.00	0.0	<0.1
Elliptio crassidens crassidens (Lamarck, 1819)	0.28	0.00	0.0	0.0
Elliptio dilatata (Rafinesque, 1820)	1.54	3.20	0.8	2.2
Subfamily Lampsilinae				
Obliquaria reflexa Rafinesque, 1820	0.55	3.02	1.2	2.1
Actinonaias ligamentina carinata (Barnes, 1823)	3.72	0.53	<0.1	<0.1
Ellipsaria lineolata (Rafinesque, 1820)	0.62	0.36	0.0	0.1
Obovaria olivaria (Rafinesque, 1820)	2.56	0.36	1.4	0.9
Truncilla truncata Rafinesque, 1820	0.13	2.04	1.0	5.3
Truncilla donaciformis (Lea, 1827)	0.00	0.09	0.9	6.7
Leptodea fragilis (Rafinesque, 1820)	0.00	4.44	<0.1	4.8
Potamilus alatus (Say, 1817)	0.05	6.39	0.4	2.4
Potamilus ohiensis (Rafinesque, 1820)	0.00	0.00	0.0	0.1
Potamilus capax (Green, 1832)	0.00	0.09	0.0	0.0
Toxolasma parvus (Barnes, 1823)	0.00	0.00	0.0	<0.1
Ligumia recta (Lamarck, 1819)	0.11	0.53	0.1	0.6
Lampsilis teres teres (Rafinesque, 1820)	0.02	47.51	0.0	0.0
Lampsilis teres anodontoides (Lea, 1831)	0.00	0.27	0.0	<0.1
Lampsilis radiata luteola (Lamarck, 1819)	0.07	5.68	0.0	0.4
Lampsilis higginsi (Lea, 1857)	0.10	0.09	0.1	0.3
Lampsilis ventricosa (Barnes, 1823)	0.08	0.71	0.3	1.6
	99.97	100.00	101.0	100.2

proximately 44 species of freshwater mussels that are known to have occurred in the Pool 10 area of the UMR, in contrast to the 28 taxa represented in the described prehistoric assemblages. This disparity of 16 species appears to be due in part to a bias by prehistoric harvestors against mussel taxa having a small adult shell size which were uncommon in all assemblages. In the subfossil assemblages, no individuals of *Toxolasma parvus* (Barnes, 1823) or *Truncilla donaciformis* (Lea, 1827) were recovered, while both species are presently widespread and locally common in the Pool 10 area. Mussel species having a slightly larger shell size, *e.g.*, *Truncilla truncata* and *Obliquaria reflexa* are rare, but persistent in the subfossil assemblages. Juveniles of any taxon were rare or absent in the assemblages. It is assumed that small shelled individuals were not harvested as a food source at the sites considered, indicating a cultural bias towards large shelled species or individuals.

Other factors possibly influencing the species composition of the subfossil assemblages include water depth, which may have restricted prehistoric mussel harvesting to depths suitable for hand collecting. Any species that were preferentially deep water forms, may be disproportionately rare. Additionally, species characteristic of a low velocity current or backwater habitats with soft substrates (*e.g.*, some Anodontinae) are rare or absent in the described assemblages.

Finally, it is probable that a number of species, in addition to the previously discussed *A. plicata* and *M. nervosa*, have dramatically increased in number or expanded their range northward in the UMR under the influence of the large scale habitat modifications of recent decades. This appears to be the case for *Anodonta suborbiculata*, Say, 1831 (Havlik, 1981), and is perhaps true for *T. parvus* and *T. donaciformis*. Other species recorded historically have always been rare and have a sharply circumscribed habitat preference (*e.g.*, *Cumberlandia monodonta* (Say, 1829) and *Simpsonaias ambigua* (Say, 1825)), or are extralimital when encountered in the main stem UMR (*e.g.*, *Alasmidonta marginata*, Say, 1818). These taxa are not unexpectedly absent from the prehistoric assemblages.

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LITERATURE CITED

Baker, F. C. 1903. Shell collecting on the Mississippi. The Nautilus 16:102–105.

Baker, F. C. 1905. The molluscan fauna of McGregor, Iowa. Transactions of the Academy of Science of St. Louis 15(3): 249–258.

Coker, R. E. 1914. Water-power development in relation to fishes and mussels of the Mississippi. U.S. Department of the Interior, Washington, DC, Bureau of Fisheries, Document No. 805, Appendix VIII, 28 p.

Coker, R. E. 1919. Fresh-water mussels and mussel industries of the United States. U.S. Department of the Interior, Washington, DC, Bureau of Fisheries Bulletin 36:13–89.

Coker, R. E. 1930. Studies of common fishes of the Mississippi River at Keokuk. U.S. Department of the Interior, Washington, DC, Bureau of Fisheries Bulletin 45:141–225.

Coker, R. E., A. F. Shira, H. W. Clark, and A. D. Howard 1921. Natural history and propagation of fresh-water mussels. U.S. Department of the Interior, Washington, DC, Bureau of Fisheries Bulletin 37:76–181.

Duncan, R. E. and P. A. Thiel. 1983. A survey of the mussel densities in Pool 10 of the Upper Mississippi River. Wisconsin Department of Natural Resources, Technical Bulletin No. 139, Madison, WI, 14 p.

Ellis, M. M 1936. Erosion silt as a factor in aquatic environments. Ecology 17(1):29–42.

Fuller, S. L. H 1980. Historical and current distributions of fresh water mussels (Mollusca: Bivalvia Unionidae) in the Upper Mississippi River. *In:* Rasmussen, J L. (ed.). Proceedings of the UMRCC [Upper Mississippi River Conservation Committee] Symposium on Upper Mississippi River bivalve mollusks. Upper Mississippi River Conservation Committee, Rock Island, IL, p. 72–119.

Grier, N. M. 1926. Report on the study and appraisal of mussel resources in selected areas of the Upper Mississippi River, 1920–25. American Midland Naturalist 10(1):89–110, 113–134.

Havlik, M E. 1981. The northern extension of the range of *Anodonta suborbiculata* Say (Bivalvia: Unionidae). The Nautilus 95(2):89–90.

Havlik, M. E. 1983. Naiad mollusk populations (Bivalvia: Unionidae) in Pools 7 and 8 of the Mississippi River near La Crosse, Wisconsin American Malacological Bulletin 1: 51–60.

Havlik, M. E. and D. H. Stansbery. 1978. The naiad mollusks of the Mississippi River in the vicinity of Prairie du Chien, Wisconsin. Bulletin of the American Malacological Union 1977:9–12.

Knott, M. J 1980. The pearl button industry and its impacts on Mississippi River mussel fauna. *In:* Rasmussen, J. L. (ed.). Proceedings of the UMRCC [Upper Mississippi River Conservation Committee] Symposium on Upper Mississippi River bivalve mollusks. Upper Mississippi River Conservation Committee, Rock Island, IL, p. 11–16.

Kunz, G. F. 1898. The fresh-water pearl and pearl fisheries of the United States. Bulletin of the United State Fisheries Commission 17:375–426.

Marsh, W. A. 1887. Brief notes on the land and fresh-water shells of Mercer Co., Ill. The Conchologist Exchange 1 (No. 9 and 10).

Mathiak, H A 1979. A river survey of the unionid mussels of Wisconsin 1973–1977. Sand Shell Press, Horicon, WI, 75 p.

Morrison, J. P. E. 1942. Preliminary report on mollusks found in the shell mounds of the Pickwick Landing Basin in the Tennessee River Valley. *In:* Webb, W. S. and D. L. DeJarnette. An archeological survey of Pickwick Basin in the adjacent portions of the states of Alabama, Mississippi and Tennessee. Bureau of American Ethnology Bulletin 129, Washington, DC, p. 337–392.

Oesch, R D 1984. Missouri naiades: a guide to the mussels of Missouri. Missouri Department of Conservation, Jefferson City, MO, 270 p.

Parmalee, P. W. 1967. The fresh-water mussels of Illinois. Popular Science Series, Vol. VIII. Illinois State Museum, 108 p.

Parmalee, P. W. and A. E. Bogan. 1986. Molluscan remains from aboriginal middens at the Clinch River breeder re-

actor plant site, Roane County, Tennessee. American Malacological Bulletin 4(1):25–37.

Parmalee, P. W., W. E. Klippel, and A. E. Bogan. 1980. Notes on the prehistoric and present status of the naiad fauna of the Middle Cumberland River, Smith County, Tennessee. The Nautilus 94(3):93–105.

Parmalee, P. W., W. E. Klippel, and A. E. Bogan. 1982. Aboriginal and modern freshwater mussel assemblages (Pelecypoda: Unionidae) from the Chickamauga Reservoir, Tennessee. Brimleyana 8:75–90.

Perry, E. W. 1979. A survey of Upper Mississippi River mussels. *In:* Rasmussen, J. L. (ed.). A compendium of fishery information on the Upper Mississippi River, second edition. Upper Mississippi River Conservation Commission, Rock Island, IL, p. 118–139.

Pratt, W. H. 1876. List of land and fresh water shells found at Davenport, Iowa. Proceedings of the Davenport Academy of Natural Science 1:165–168.

Rasmussen, J. L. 1979. Description of the Upper Mississippi River. *In:* Rasmussen, J. L. (ed.). A compendium of fishery information on the Upper Mississippi River, 2nd ed. Upper Mississippi River Conservation Commission, Rock Island, IL, p. 3–20.

Shimek, B. 1888. The mollusca of eastern Iowa. Iowa University Natural History Bulletin 1:56–81.

Smith, H. M. 1899. The mussel fishery and pearl-button industry of the Mississippi River. U.S. Fisheries Commission Bulletin 1898, 18: 289–314.

Stansbery, D. H. 1965. The molluscan fauna. *In:* Prufer, O. H. (ed.). The McGraw Site: a study in Hopewellian dynamics. Cleveland Museum of Natural History, Scientific Publications, No. 4, p. 119–124.

Stansbery, D. H. 1982. A list of the unionid mollusks of the Ohio River system. The Ohio State University Museum of Zoology Reports for 1982, No. 4.

Stevenson, K. P. 1985. Oneota subsistence-related behavior in the driftless area: a study of the Valley View site near La Crosse, Wisconsin. Doctoral dissertation, Department of Anthropology, University of Wisconsin–Madison, 601 p.

Surber, T. 1913. Notes on the natural hosts of fresh-water mussels. U.S. Bureau of Fisheries Bulletin 32:101–116.

Taylor, R. W. and B. D. Spurlock. 1982. The changing Ohio River naiad fauna: a comparison of early Indian middens with today. The Nautilus 96(2):49–51.

Theler, J. L. 1983. Woodland tradition economic strategies: animal resource utilization in southwestern Wisconsin and northeastern Iowa. Doctoral dissertation, Department of Anthropology, University of Wisconsin–Madison, 433 p.

Thiel, P. A. 1981. A survey of unionid mussels in the Upper Mississippi River (Pools 3–11). Wisconsin Department of Natural Resources, Technical Bulletin No. 124, Madison, WI, 25 p.

Van der Schalie, H. and A. Van der Schalie. 1950. The mussels of the Mississippi River. American Midland Naturalist 44(2): 448–466.

Van Dyke, A., D. F. Overstreet, and J. L. Theler. 1980. Archaeological recovery at 11-RI-337, an early Middle Woodland shell midden in East Moline, Illinois. The Wisconsin Archeologist 61(2):125–256.

Witter, F. M. 1883. The mollusca of Muscatine County and vicinity. The Muscatine Conchological Club, Muscatine, Iowa, S. W. Cassino and Company, Boston, 24 p.

Henry Drummond Russell (1908–87) with a Bibliography of His Malacological Publications and a List of New Taxa Introduced by Him

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The Mollusk Department of the Museum of Comparative Zoology at Harvard University regretfully announces that our colleague, Dr. Henry Drummond Russell, died on January 24, 1987 at the age of 78 after a long illness; tragically, his wife, Elizabeth Meade Russell, subsequently died on February 24, 1987. His immediate family, including his three daughters, Louise Russell, Barbara R. Williams, and Cynthia R. Howe, and all their friends and colleagues grieve these losses.

Henry was born in Boston on September 5, 1908, the son of Charles Theodore Russell and Louise Rust. After his preparatory education at Miss Woodward's School in Boston, the Longwood Day School in Brookline, and the Middlesex School in Concord, Massachusetts, he enrolled at Harvard College in 1928, graduated in 1932 with an A.B. degree, and took his Master's and Doctoral degrees at Boston University in 1933 and 1940.

After graduation from Harvard in the midst of the Depression Henry did volunteer work in the Mollusk Department which, of course, brought him into close association with Dr. William J. Clench, the then curator; this experience also facilitated his study of the prosobranch gastropod family Neritidae in the western Atlantic, a topic which constituted his doctoral dissertation. Several field trips occupied Henry's energies during the summer months in the thirties when he accompanied Dr. Clench and others to the West Indies: in 1934 to northern Cuba; in 1935 and 1936 to Cat Island and Long Island in the Bahamas; and in 1937 to Puerto Rico as well as to the northern portion of Santo Domingo, particularly the Bahía de Samana, Puerto Plata, and Monte Cristi on the island of Hispaniola. One recalls the gusto with which Henry and Bill would relate various anecdotes of these adventurous expeditions. Once, in Oriente, in the dining room of a small pension in which a dog snoozed in the corner, Henry, who was the acknowleged official translator since he knew several words of Spanish, was instructed by Bill to ask the waiter what was to be the dessert that evening. Henry did so and to their surprise, the waiter turned on his heel, marched across the room and kicked the dog out. What actually Henry had said in Spanish was never discovered. These field trips

resulted in the collection of natural history specimens for the museum, particularly a large series of terrestrial, freshwater, and marine mollusks.

During the summer of 1938, Henry worked with the Department of Fish and Game of New Hampshire, making a survey of the Merrimack River watershed and its central lakes and streams to determine the feasibility for stocking them with fish; these field collections and studies resulted in the publication, with W. J. Clench, of papers on the freshwater mollusks of the Merrimack and Connecticut River watersheds (see Bibliography).

Granted the title of Honorary Assistant Curator of Mollusks in the MCZ in 1940, Henry subsequently joined the Division of Marine Fishes in the Department of Conservation of Massachusetts as Assistant Biologist where he was involved in a state aid project for the restocking and cultivating of the clam flats of coastal Massachusetts; he resigned this position in March, 1942.

From June, 1942 to March, 1943, he was Assistant to Dr. Thomas Barbour, the President of the New England Museum of Natural History, now the Museum of Science. For two months in the spring of 1943, as a participant in the war effort, Henry collaborated with Dr. Charles H. Blake at the Massachusetts Institute of Technology in an Army study of insect pests in supplies. Then from September, 1943 to October, 1944 he was involved with a study, supported by the United States Navy, of submarine illumination with Dr. George L. Clarke at the Woods Hole Oceanographic Institution.

Then Henry began work at the Fatigue Laboratory at Harvard where studies were conducted on various aspects of human physiology under the stress of thermal extremes, especially on conditions affecting men working in very cold climates. From 1947 to 1948, he pursued studies on boring and fouling organisms at the William F. Clapp Laboratories in Duxbury, Massachusetts.

In 1948, Henry commenced a long association with Boston University when he was appointed as Instructor in General Biology. An effective and enthusiastic teacher, he assumed charge of the General Biological Laboratories which introduced Freshmen to the subject; he lectured on evolution, genetics, and several other subjects. During the summer of 1952, he conducted a survey of Spy Pond in Arlington under the auspices of the Massachusetts Department of Public Health. From the fall of 1952 until 1961 he was Assistant Professor of Biology when he once again returned to research as an Associate of the newly established Systematics and Ecology Program at the Marine Biological Laboratories at Woods Hole. Here he published his useful handbook on laboratory techniques for narcotizing and preserving animals for future study.

He was president of the Boston Malacological Club 1936–38, 1940–42, and 1957–59 and for many years served as its Conchological Recorder, a role in which he excelled and one in which he both educated and entertained his audience with his superb sense of humor; he became Councillor-at-Large for the American Malacological Union in 1971, and was active in the American Association for the Advancement of Science as well as being a member of the corporation of the Bermuda Biological Station and the secretary of the Cape Cod Shellfish Corporation.

Relatively late in his career, Henry culminated his work on the group of animals he enjoyed most with his book *Index Nudibranchia*, which was published in 1971 by the Delaware Museum of Natural History. This indispensable contribution consists of a delineation of all the scientific papers published on this unique group of basically shell-less snails from the time of Belon and Rondelet in the middle of the sixteenth century to 1965. It also comprises a catalogue of all taxonomic names applied to these animals, including especially their generic and specific epithets alphabetically arranged; special indices are provided to assist a researcher in studying the geographic ranges and natural history of these animals. A special supplement, covering the literature on nudibranchs between 1966 and 1975 was published in the summer of 1986 by the Department of Mollusks in the MCZ, of which he had been an Associate since 1972.

Henry was always actively supportive of civic affairs in his home town of Dover, Massachusetts. He was a member of the Town Warrant Committee in 1941, the Dover Conservation Commission, and chairman of the Public School Association in 1946; additionally, he supported enthusiastically other conservation oriented organizations, including the Hale Reservation of Westwood and the Neponset Conservation Association, of which he served as director in 1975.

BIBLIOGRAPHY OF THE MALACOLOGICAL PUBLICATIONS OF H. D. RUSSELL[1]

1935a. Some nudibranchs of Bermuda, with a description of a new species. The Nautilus 49(2):59–61, pl. 4 (October).

1935b. *Coryphella pellucida* Alder & Hancock. The Nautilus 49(2):65–66 (October).

1937a. Living rainbows of the sea. Bulletin of the New England Museum of Natural History No. 82:3–5, text fig. (January).

1937b. *Cratena veronica* Verrill. The Nautilus 50(4): 142 (April).

1938. Freshwater shells of New Hampshire. *In:* Biological survey of the Merrimack Watershed. New Hampshire Fish and Game Department, Concord, NH, Survey Report No. 3:201–206, pls. A and B, text fig. 1 (with William J. Clench as senior author) (December).

1940a. Freshwater shells of New Hampshire. *In:* Biological survey of the Connecticut Watershed. New Hampshire Fish and Game Department, Concord, NH, Survey Report No. 4:222–227, pls. III–IV, text figs. 83–84 (with William J Clench as senior author) (March).

1940b. The Recent mollusks of the family Neritidae of the West Indian Region. Abstract of a dissertation, Boston University Graduate School, Boston, MA, 3 p. (May).

1940c. Mr. B. wants better fishing. New England Naturalist No. 7:19–23 (June).

1940d. Freshwater shells of New Hampshire. The Nautilus 54(2):52–53 (with William J Clench as senior author) (October).

1940e. Some new Neritidae from the West Indies. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 14(4):257–262, pl. 46 (December).

1941. The Recent mollusks of the family Neritidae of the Western Atlantic. Bulletin of the Museum of Comparative Zoology, Harvard College 88(4): 347–404, pls. 1–7, text figs. 1–4 (August).

[1] Excluded are the numerous literature reviews, entitled the 'Article of the month', which appeared in the New York Shell Club News from September 1972 until 1979.

1942a. Observations on the feeding of *Aeolidia papillosa* L., with notes on the hatching of veligers of *Cuthona amoena* A. & H. The Nautilus 55(3): 80–82 (January).

1942b. A new species of *Onchidiopsis* from Baffin Land. National Research Council of Canada, Canadian Journal of Research 20:50–55, text figs. 1–9, 1 table (February).

1944. A stitch in time. The Nautilus 58(1):32–33 (July).

1946. Ecologic notes concerning *Elysia chlorotica*, Gould and *Stiliger fuscata*, Gould The Nautilus 59(3):95–97 (January).

1951. Seasonal distribution of *Najadicola ingens* (K.) (Acarina) in a New Hampshire pond. Psyche 58(3):111–119, graphs 1–6, table 1 (with Arthur G. Humes as senior author) (September).

1952. The Duxbury Bay 1950 set of *Mya arenaria* L. The Nautilus 66(1):7–10, text fig. 1 (July).

1955. A new clam industry in New England. The Nautilus 69(2):53–56 (October).

1960. Heteropods and pteropods as food of the fish genera, *Thunnus* and *Alepisaurus*. The Nautilus 74(2):46–56, map, lists 1–3, tables 1–3 (October).

1963. Notes on methods for the narcotization, killing, fixation, and preservation of marine organisms. Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, MA, 70 p. (April).

1964. New England nudibranch notes. The Nautilus 78(2):37–42, table 1 (October).

1966. Kelaart's Ceylon opisthobranch species. The Nautilus 79(4):120–122 (April).

1967. Some nudibranch names. Thirty-second Annual Meeting, The American Malacological Union, Inc., Annual Reports for 1966, Bulletin 33:38–39 (abstract) (probably January). [Although at the end of the Table of Contents a date of December 1, 1966 is given, normally these were not mailed or distributed until early the following year; beginning with Bulletin 34 the mailing date is given.]

1968a. *Chromodoris californiensis* and *C. calensis* (Notes and News). The Nautilus 81(4):140–141 (April).

1968b. A bibliography of nudibranchiate interstitial fauna. Psammonalia (Newsletter of the Association of Meiobenthologists), No. 6:11–13 (November). [Psammonalia states on its cover: This document is not part of the scientific literature and is not to be cited, abstracted or reprinted as a published document.]

1969. Interstitial opisthobranchs from North America. American Zoologist. Vol. 9(4):615 (with Donald J. Zinn as senior author) (November).

1971a. A type of Nudibranchia bibliography. Thirty-sixth Annual Meeting, The American Malacological Union, Inc., Annual Reports for 1970, Bulletin 37:56–57 (abstract) (February).

1971b. Index Nudibranchia. A catalog of the literature 1554–1965. The Delaware Museum of Natural History, iv + 141 p. (July).

1971c. Evolution of a nudibranch bibliography. The Echo No. 4. Abstracts and Proceedings of the Fourth Annual Meeting of The Western Society of Malacologists, Pacific Grove, CA, June 16–19, 1971, p. 28 (December).

1971d. A list of the nudibranchs of India and adjacent seas. Symposium on Indian Ocean and Adjacent Seas, Cochin, India, January 12–18, 1971. Marine Biological Association of India, Abstract No. 149, Section XV, p. 91 [title only] (no month).

1977. A glimpse of Bermuda nudibranchs. Newsletter Bermuda Biological Station for Research 6(2):2 (October).

1978. Leopold and Rudolph Blaschka's nudibranch glass models. The Nautilus 92(4):167–172, fig. 1 (with Catharine G. Kessler as senior author) (October).

1979. Some shell-less New England marine snails. Aquasphere. Journal of the New England Aquarium 13(3):28–31, 6 text figs. (December).

1980. Invertebrates in glass. Aquasphere. Journal of the New England Aquarium 14(2):30–33, 4 text figs. (with Catherine [sic] G. Kessler as senior author) (September).

1986. Index Nudibranchia, Supplement I, 1966–1975. Special Occasional Publications No. 7, Department of Mollusks, Museum of Comparative Zoology, Harvard University, 100 p. (July).

NEW MALACOLOGICAL TAXA INTRODUCED BY H. D. RUSSELL

clenchi Russell 1935a. *Glossodoris*. The Nautilus 49(2): 59, pl. 4, figs. A–E (holotype, Museum of Comparative Zoology No. 109,085; type-locality, Ferry Reach [St. George], Bermuda).

clenchi Russell 1948e. *Neritina*. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 14(4):261, pl. 46, figs. 1–2 (holotype, Museum of Comparative Zoology No. 115,701; type-locality, Rio Manjon, 7 km SE of Puerto Plata, Santo Domingo).

kingmaruensis Russell 1942b. *Onchidiopsis*. Canadian Journal of Research 20:50, figs. 1–9 (holotype, Royal Ontario Museum, Toronto, No. 17,260; type-locality, Lake Harbour Fiord, Baffin Land).

piratica Russell 1940e. *Neritina*. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 14(4): 259, pl. 46, figs. 3–4 (holotype, Museum of Comparative Zoology No. 115,702; type-locality, Wounta Lagoon, Nicaragua).

weyssei Russell 1940e. *Smaragdia viridis*. Memorias de la Sociedad Cubana de Historia Natural "Felipe Poey" 14(4):257, pl. 46, figs. 5–6 (holotype, Museum of Comparative Zoology No. 88,815; type-locality, Miami, Florida).

New Names for Two Species of *Cancellaria* (Mollusca: Gastropoda)

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The purpose of this short note is to propose replacement names for two species of *Cancellaria*: *C. quasilla nomen novum* for *C. cretacea* E. A. Smith, 1899 *non* Nyst, 1881 and *C. laddi nomen novum* for *C. petiti* Ladd, 1982 *non* Olsson, 1967.

Cancellaria quasilla Petit *nomen novum*

Cancellaria cretacea E. A. Smith, 1899:245.
Not *Cancellaria cretacea* Nyst, 1881:8.
Cancellaria cretacea E. A. Smith; McArdle, 1901: pl. 11, figs. 5, 5a.

Discussion: This species is known from the holotype (figure 1), which is in the collection of the Zoological Survey of India, from 360 fathoms off the Travancore coast of south India, and from a badly broken specimen in the collection of the Academy of Natural Sciences of Philadelphia (ANSP 291936, Andaman Sea, south Burma). *Cancellaria quasilla* resembles species of *Merica* in overall form, and the columellar structure is similar to that of *C. rosewateri* Petit, 1983 from the Gulf of Mexico. It differs from species of *Merica* in that it lacks a well-defined anterior canal. A determination of subgeneric placement must await additional study on the entire family.

Etymology: From the Latin *quasillum* (dimin. of *qualum*, a wicker basket) for the woven aspect caused by the strong cords and ribs.

Comments: The holotype is refigured here. Appreciation is expressed to Dr. N. V. Subba Rao, Superintending Zoologist, Zoological Survey of India, Calcutta, for confirming the presence of the holotype in the Survey collection, and for furnishing photographs of the holotype.

Cancellaria (*Merica*) *laddi* Petit *nomen novum*

Cancellaria (*Merica*) *petiti* Ladd, 1982:57, pl. 14, figs. 16–18.
Not *Cancellaria* (*Cancellaria*) *petiti* Olsson, 1967:44

Discussion: This species is from Vanua Levu, Fiji (Pliocene; unnamed formation). As Ladd stated, it is closely related to the Recent Indo-Pacific *Cancellaria* (*Merica*) *oblonga* Sowerby, 1825, from which it differs in being more slender and much more strongly sculptured.

Figure 1. Holotype of *Cancellaria quasilla* Petit *nomen novum* (= *C. cretacea* Smith *non* Nyst). Dorsal and ventral views. Height 25 mm; width 19 mm.

Etymology: This replacement name honors the late Dr. Harry S. Ladd, with whom I enjoyed many interesting and educational conversations on the Tertiary faunas of the Indo-Pacific.

LITERATURE CITED

Ladd, H. S. 1982. Cenozoic fossil mollusks from Western Pacific Islands; gastropods (Eulimidae and Volutidae through Terebridae). U.S. Geological Survey Professional Paper 1171:1–100, pls. 1–41.

McArdle, A. F. 1901. Illustrations of the the zoology of the Royal Indian Marine Survey Ship *Investigator* . . . Mollusca: Pt. III, pls. 9–13. Calcutta.

Nyst, P. H. 1881. Conchyliologie des Terrains Tertiaires de la Belgique, Pt. 1. Annales du Musée Royal d'Histoire Naturelle de Belgique 3:1–263.

Olsson, A. A. 1967. Some Tertiary mollusks from South Florida and the Caribbean. Paleontological Research Institution, Ithaca, New York, 61 p., 9 pls.

Petit, R. E. 1983. A new species of *Cancellaria* (Mollusca: Cancellariidae) from the northern Gulf of Mexico. Proceedings of the Biological Society of Washington 96(2): 250–252

Smith, E. A. 1899. Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator' . . On Mollusca from the Bay of Bengal and the Arabian Sea. Annals and Magazine of Natural History, Ser. 7, 4:237–251.

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CONTENTS

Description of a New, Giant *Ataxocerithium* Species from Australia with Remarks on the Systematic Placement of the Genus (Prosobranchia: Cerithiopsidae)

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ABSTRACT

A new, large *Ataxocerithium* species is described and given the name *eximium*. This new species differs considerably in shell characters from any other known *Ataxocerithium* species. Shell characters, the radula, and anatomical characters, such as an acrembolic proboscis, suggest *Ataxocerithium* be assigned to the Cerithiopsidae. Comparison of the new species with other taxa is made and a brief discussion of the genus is presented.

INTRODUCTION

The genus *Ataxocerithium* Tate, 1894 is not well known. The limits and systematic position of the genus are poorly understood, and the anatomy is undescribed. The genus usually has been allocated to the Cerithiidae Ferussac (Cossmann, 1906:92; Thiele, 1929:212; Wenz, 1940:759; Powell, 1951:111; Cotton, 1959:361; Iredale & McMichael, 1962:44), and recently to the Cerithiellidae Golikov and Starobogatov (Marshall, 1978:60). A cursory examination of the many species attributed to this taxon suggests that *Ataxocerithium, sensu lato*, probably comprises several genera. The alpha taxonomy of this group has not been accomplished; consequently, the full extent of this radiation is not known nor is the geographic distribution of the group and its component species understood.

While studying Pacific and Indian Ocean *Ataxocerithium* species, specimens of a large, distinctive, undescribed species, dredged in deep water off Sydney, New South Wales, Australia were examined in the Australian Museum, Sydney. Much of the material was preserved in alcohol and, although the body whorls were poorly preserved, was suitable for dissection and study of the radula, operculum, and gross anatomy. Unfortunately the state of the pallial gonoducts was not able to be determined. The gross anatomy of another species, *A. scrupulosum* Iredale, 1936, was also examined and compared with the new species, and a tentative diagnosis of *Ataxocerithium* was formulated. Most *Ataxocerithium* species have relatively small shells, not exceeding 20 mm in length. The discovery of this large, distinguished species enriches our concept of this group and thus merits a full description.

MATERIALS AND METHODS

Material examined: A total of 21 specimens were examined (AMS = Australian Museum, Sydney): R.V. *TANGAROA*, Sta. U220, 32°59′S, 152°33.5′E, 381–444 m, off Newcastle, NSW (AMS c142398, c142391); R.V. *TANGAROA*, Sta. U208, 34°13.8–15.8′S, 151°26.6′–29.1′E, 381–395 m, S of Sydney, NSW (AMS c142391); FRV *KAPALA*, 39°45′S, 151°49–50′E, 439 m, off Sydney, NSW (AMS c142392); FRV *KAPALA*, Sta. K75-12-06, 34°16–21′S, 151°24–28′E, SE of Botany Bay, NSW (AMS c142394, type-lot); FRV *KAPALA*, Sta. K75-05-07, 412 m, 34°28–34′S, 151°17–19′E, E of Pt. Kembla, NSW (AMS c142396); FRV *KAPALA*, Sta. K75-12-07, 421 m, 33°43–48′S, 151°48–51′E, E of Sydney, NSW (AMS c142395); FRV *KAPALA*, Sta. K75-12-05, 34°32–39′S, 151°15–19′E, 412 m, E of Kiama, NSW (AMS c142393) (all Australia).

Methods: Three specimens were extracted from their shells, dissected, and examined under a Wild M-8 dissecting microscope. Only the head-foot and lower mantle cavity were well preserved. Radulae, protoconchs, and opercula were studied with electron microscopy using a Zeiss Novascan-30 instrument. The shells of all 21 specimens were studied, but as many of these were damaged or immature, only seven adult, complete shells, with fully developed apertures, were measured to establish the range of variation (Table 1).

SYSTEMATIC RESULTS

Superfamily **Cerithiopsacea** H. and A. Adams, 1853
Family **Cerithiopsidae** H. and A. Adams, 1853

Genus *Ataxocerithium* Tate, 1894

Diagnosis: Shell turreted, whorls inflated, sculptured with axial ribs and spiral cords. Body whorl wide with

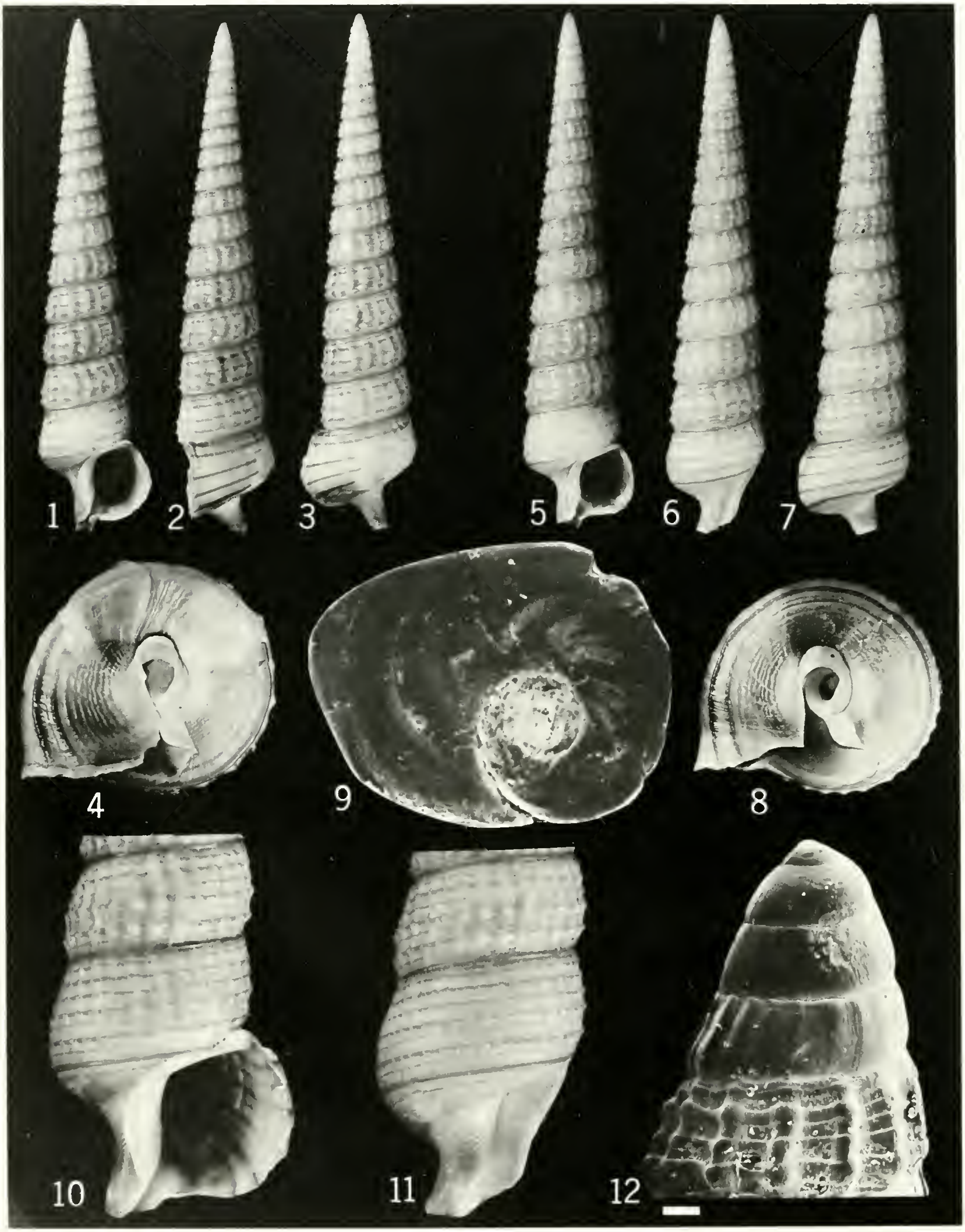
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Table 1. Range of measurements in seven adult shells of *Ataxocerithium eximium* new species.

Statistic	Length	Width	Aperture length	Aperture width	No. axial ribs	No. spiral cords	No. whorls
$\bar{x}$	43.2	9.5	6.8	5.9	22.7	4.7	20.7
SD	2.67	0.51	0.37	0.59	2.5	1.3	0.49
Range	40.1–46.3	8.7–10.1	6.5–7.2	4.9–6.6	20–27	5–6	20–21

flattened base and short, tubular anterior canal. Aperture ovate, with large columellar lip that joins base of outer apertural lip forming nearly complete peristome. Operculum corneous, ovate, paucispiral with subcentral nucleus. Foot with deep, anterior mucus gland, long, deep, longitudinal cleft; sole demarcated from foot by deep groove. Mantle edge smooth. Taenioglossate radula with long, brush-like denticles on tip of marginal teeth. Cuticular anterior esophagus in some species. Acrembolic proboscis and large esophageal gland present.

Ataxocerithium eximium new species
(figures 1–16)

Diagnosis: Large, thin, high-spired shell with cancellate, prickly sculpture due to 5 thin, beaded, spiral cords crossed by numerous collabral axial riblets. Thin, golden-tan spiral lines overlay silky-cream finish. Aperture ovate-circular with high concave columellar lip closely adpressed to lower outer lip. Long tubular anterior canal. Foot with deep longitudinal cleft. Sole separated from foot by deep cleft around its circumference. Columellar muscle long, strap-like. Osphradium a tall ridge. Acrembolic proboscis with short introvert, large jaws, cuticular anterior esophagus, long buccal mass, and long, taenioglossate radula. Esophageal gland large.

Description: *Shell (figures 1–8, 10–12; table 1):* Shell long, high-spired, slender, reaching 46.3 mm in length and 10.1 mm in width, and comprising 20–21 moderately inflated whorls. Protoconch (figure 12) of 3 smooth, inflated whorls, earliest one pointed. First teleoconch whorl sculptured with numerous axial riblets. Teleoconch (figures 1–3, 5–7) sculpture of overall cancellate, prickly, rasp-like, appearance due to 5–6 spiral cords crossing over numerous, collabral, axial riblets. Pointed beads appear where axial riblets cross spiral cords and are aligned colabrally in opisthocyrt growth lines. Earlier teleoconch whorls (figure 12) dominated by wide axial ribs and 4 weak spiral cords. Later teleoconch whorls have 7 spiral cords, 3 of which are major and 4 minor. Minor cords are on interspaces between major cords. Axial riblets less pronounced on later whorls. Penultimate whorl with 20–27 axial riblets and with fine spiral threads on first 2 adapical interspaces between major spiral cords. Suture distinct, straight, bordered with presutural and postsutural smooth, spiral cords. Body whorl (figures 10, 11) with 7 weakly beaded, nearly smooth spiral cords and fine axial growth lines. Siphonal constriction at whorl base (figures 10, 11) with numerous, fine spiral striae. Aperture (figure 10) ovate-circular, slightly longer than wide, and a little more than one-fifth the shell length. Columella concave with high columellar lip (figure 11). Anterior siphonal canal long, tubular, reflected to left of shell axis and tightly constricted from the aperture where base of columellar lip meets base of curved, convex outer lip (figure 4). Outer lip smooth and thin. Border of outer lip and columellar lip form subcircular aperture mouth. Shell color silky cream, the spiral cords a golden-tan-orange color with white beads, the suture defined by broader golden-tan, spiral cord. Periostracum not evident. Operculum (figure 9) thin, corneous, brown and paucispiral with subcentral nucleus.

Radula (figures 13–16): Radular ribbon taenioglossate, long, about $\frac{1}{12}$ the shell length. Rachidian tooth (figure 15) with square basal plate, pair of tiny basal cusps, and straight base. Anterior face of rachidian tooth strongly convex. Cutting edge with sharp, central, major cusp flanked on each side by four tiny denticles. Lateral tooth (figures 14, 15) large, robust, roughly rectangular shaped, with thick central shaft and supporting longitudinal ridge. Tip or main cusp of lateral tooth large, pointed, flanked by strong inner buttress-like cusp and with 2–3 tiny, sharp, outer denticles. Basal plate of lateral tooth broad with pointed, outer, posterior corner and longitudinal basal butress ending in slight bulge. Outer front edge of lateral tooth with medial-basal flange. Marginal teeth (figure 16) long, rod-shaped, with broad bases, brush-like apices, and long, sharp tips. Inner marginal tooth

←

Figures 1–12. *Ataxocerithium eximium* new species. **1–3.** Holotype, AMS C142394 (45.7 mm length), showing apertural, right lateral, and dorsal views. **4.** Shell base of holotype, showing close apposition of columellar lip and outer lip base (figure length 10.5 mm). **5–7.** Paratype (USNM 862328, 41 mm length), showing apertural, left lateral, and dorsal views. **8.** Shell base of paratype. **9.** Free side of operculum (4.3 mm length). **10.** Detail of aperture and body whorl, showing large columellar lip, long anterior siphon and cancellate whorl sculpture (figure length, 15 mm). **11.** Left lateral detail of body whorl showing extended columellar lip and cancellate whorl sculpture (figure length, 15 mm). **12.** SEM of papillate, smooth protoconch and early sculpture of first teleoconch whorls (bar = 200 μm).

Figures 13–16. Radula of *Ataxocerithium eximium* new species. **13.** Radular ribbon with marginal teeth folded back to show rachidian and lateral teeth (bar = 20 μm). **14.** Radular ribbon tilted to expose undersurfaces of rachidian and lateral teeth (bar = 20 μm). **15.** Details of rachidian and lateral teeth (bar = 10 μm). **16.** Details of marginal teeth showing brush-like tips (bar = 10 μm).

apex with 5 inner flanking, needle-shaped denticles and 2–3 sharp, outer flanking denticles. Outer marginal tooth same, but with only 1 outer flanking denticle.

Animal (figure 17): Preserved animal pink. Foot long, separated from sole by wide, deep furrow around its entire edge (figure 17, fs). Propodium broad, crescent shaped anteriorly, and with dorsal surface pigmented dark brown. Deep propodial mucus gland at leading edge of sole (figure 17, pmg). Sole of foot light pink and with many transverse wrinkles; divided longitudinally by deep cleft (figure 17, cs) that begins just behind propodial mucus gland. Head has broad, short, muscular snout (figure 17, sn) with bilobed tip and mouth (figure 17, m) leading to large introvert. Pair of long cephalic tentacles (figure 17, t) each with large eye (figure 17, e) at outer peduncular base. Eyes black with red center. Mantle edge (figure 17, me) smooth. Very long, strap-like columellar muscle extends posteriorly for 5.5 whorls. Mantle cavity large, spacious. Osphradium a long, high, narrow, white ridge, slightly swollen at its base and thinly tapered at its dorsal edge. Ctenidium large, adjacent to osphradium and comprised of long, finger shaped, triangular filaments. Hypobranchial gland moderately developed. Rectum wide. Pallial gonoduct thick and glandular. Acrembolic proboscis present: Introvert short, somewhat cuticular interiorly; separated from opening of mouth by circular band of muscles. Pair of large (1 mm long), oval-rectangular jaws with scaly surface in oral cavity. Buccal mass elongate and with long, taenioglossate radular ribbon, which emerges distally from beneath right side of buccal mass, crosses over it and lies on left side of esophagus. Anterior esophagus appears to be cuticularized. Pair of large, orange, ascinous salivary glands present; left gland larger and extends partially through nerve ring; right gland smaller, and lies anterior to nerve

ring. Large mid-esophageal gland with inner epithelium thrown into many thin transverse filaments that appear to extend the entire esophageal circumference. Nervous system epiathroid. Thin, short, but distinctive connectives between cerebral and pleural ganglia. Right pleural ganglion about one-half the size of right cerebral ganglion and with long supraesophageal connective. Left pleural ganglion with short connective to subesophageal ganglion. Long connectives join pleural ganglia to anteriorly located pedal ganglia.

Holotype: AMS C142394, length 45.7 mm, width 10.1 mm; 5 paratypes, AMS C153005; 2 paratypes, USNM 862328.

Type locality: Dredged 421 m, 34°21–16′S, 151°24–28′E, SE of Botany Bay, NSW, Australia.

Etymology: From the Latin adjective, *eximius, a, um*, distinguished, extraordinary.

DISCUSSION

This large, many-whorled, unusually sculptured species is the largest known *Ataxocerithium* species, and not easily confused with any other congener. Four other nominate sympatric species of *Ataxocerithium* occur off New South Wales (Iredale & McMichael, 1962:44), and these are all appreciably smaller. The high spired shell and silky-cream ground with its thin, golden-tan, spiral lines, and the fine, prickly, cancellate sculpture (figures 10–12) readily distinguish *A. eximium*. The highly turreted cerithiid species, *Cerithium matukense* Watson, 1886, looks very much like *A. eximium*, but differs in having weaker collabral axial riblets, straight sided whorls, and lacks the protruding columellar lip joining the lower outer lip, and the smooth papillate protoconch of the latter taxon. *Ataxocerithium eximium* does not appear to vary much in sculpture (see table 1), but the only known specimens are all from a narrow locale.

Ataxocerithium eximium, to date, has been dredged on soft bottoms in depths of about 380–450 m, from a narrow geographic range off the coast of Sydney, New South Wales. It probably occurs in similar habitats and depths along the southeastern Australian coast. Some shells are covered by a thin growth of sponge. The rectum was filled with gray sediment and detritus comprising arthropod appendages, bryozoan pieces, foraminiferans, sand grains and sponge spicules. This species probably lives and feeds on sponges, as does *Ataxocerithium scrupulosum* Iredale, 1936, which has been collected on sponges by SCUBA divers (Ian Loch, personal communication). Most cerithiopsids appear to be sponge feeders. No drilled shells have been seen. Shells frequently have broken apertures suggesting predation by crabs or fish.

Ataxocerithium eximium differs so much from any other congener that it might be considered representative of a new genus. While there appear to be major differences in shell and radular morphology among various *Ataxocerithium* species (personal observation), the group has never undergone revision nor has the internal anatomy been seriously studied. Although I have examined the anatomy of two species, all species are best referred to *Ataxocerithium*, *sensu lato*, until the group is more comprehensively known.

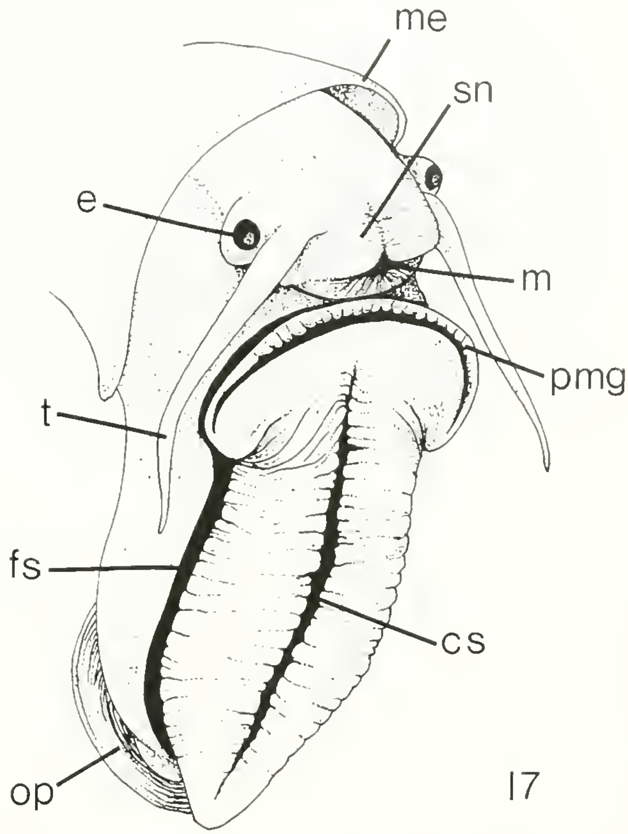

Figure 17. Head-foot of *Ataxocerithium eximium*. Abbreviations: cs = longitudinal cleft in sole of foot; e = eye; fs = furrow separating foot from sole; m = mouth; me = mantle edge; op = operculum; pmg = propodial mucus gland; sn = snout; t = cephalic tentacle.

Powell's (1951:191, fig. 1 (34)) figure of the radula of *Ataxocerithium pullum* (Philippi, 1845), the only other published figure of the radula of an *Ataxocerithium* species known to me, resembles the general morphology of the rachidian and lateral teeth of *A. eximium* shown herein, although the marginal teeth of *A. pullum* look quite different. I have studied the radula of another *Ataxocerithium* species from Natal, South Africa, in which the radular teeth differ in shape and cusp number from those of *A. eximium*, in every aspect. Thus, there is probably a wide range of variation in radular morphologies in this group.

Although most authors have placed *Ataxocerithium* in the Cerithiidae, the radula of *A. eximium* is more indicative of those of cerithiopsids (superfamily Cerithiopsacea). However, as mentioned above, *Ataxocerithium* radular morphology is variable. Marshall (1978: 60) stated that his preliminary studies of Australasian species of *Ataxocerithium* suggest that the genus should be referred to the Cerithiellidae Golikov and Starobo-

gatov, 1975, but presented no supporting data. The Cerithiellidae is a poorly defined group: to my knowledge, no author has listed the apomorphic characters defining this group or has established its familial status with any supporting data. The radula of *Cerithiella metula* Loven, as depicted by Sars (1878: table 7, fig. 4), differs markedly from that of *A. eximium* in lacking the pair of basal denticles and in having fewer cusps on the cutting edge of the rachidian tooth. In *A. eximium*, the base of the lateral tooth is much longer and has a basal ridge; moreover, the marginal teeth are long and with brush-like tips, while they are simple, short hooks in *Cerithiella metula*. Marshall (*in litt.*) has suggested that the two large cusps on the lateral tooth of *Ataxocerithium* and *Cerithiella* are homologous and that the *Cerithiella* radula originated by reduction from an *Ataxocerithium*-like plan, but available data on both taxa are too few to allow anything other than speculation about radular evolution, at this point. Marshall (1980:85) subsequently regarded the Cerithiellidae as a subfamily of the Triforidae Jousseaume (Cerithiopsidae). The Triforidae, largely based on shell characters, is another poorly defined, higher category taxon, which lacks the salient autapomorphies necessary for familial status. While agreeing with Marshall's proposed scheme of relationships, I disagree with the ranking. As so little is known about the taxa *Cerithiella* and *Triforis* Deshayes, other than conchology, it seems premature and non-parsimonious to accord them familial or even subfamilial status. They are best regarded as higher category taxa of uncertain status within the Cerithiopsidae.

The protoconch (figure 12) of *Ataxocerithium eximium* is quite different from the protoconch of the *Ataxocerithium* species depicted by Marshall (1980:86, fig. 1, F), which closely resembles that of a *Triforis* species depicted in the same figure. It seems that there is wide variation in *Ataxocerithium* protoconch morphology. Marshall (1978:54) has pointed out the extreme diversity of cerithiopsid radulae.

The longitudinal cleft in the sole of the foot of *A. eximium* is exactly like that of *Cerithiopsis powelli* Marshall, 1978 [Marshall (1978:53, fig. 2)] (Cerithiopsidae), and very much like that depicted by Marshall (1977: 113, fig. 1, A) for *Metaxia exaltata* (Powell, 1930) (Triphoridae), and *Seila adamsii* (Lea, 1845) (Triphoridae), which I have dissected. The anatomy of the anterior alimentary canal of *A. eximium* (cuticularized anterior esophagus) and *A. scrupulosum* differs from that of other described cerithiopsids by the presence of a short, but well-developed snout. Otherwise, it is similar in layout to the alimentary canal of *Cerithiopsis* species (Cerithiopsidae), as described by Fretter (1951:567–576), and not unlike that of *Mastonia* species (Triphoridae), described by Kosuge (1966:303–305). The layout of the nervous system of *A. eximium* is also similar to that described for *Mastonia* (Kosuge, 1966:305). Thus, *Ataxocerithium* species appear to share characters found in cerithiopsids and triphorids, but have more in common with cerithiopsids. Anatomical differences described in the literature between cerithiopsids and triphorids do not justify their separation into two separate superfamilies.

In conclusion, study of the anatomy and radula of *Ataxocerithium eximium* and *A. scrupulosum* definitely excludes them from the Cerithiidae and supports their allocation to the Cerithiopsidae, superfamily Cerithiopsacea, near *Cerithiella* and *Triforis*. If it is shown that *Ataxocerithium* is a sister group to the latter two taxa, they may all comprise a separate clade within (subfamily Cerithiellinae) or separate from (Cerithiellidae) the Cerithiopsidae.

The genus *Ataxocerithium* needs much attention: current knowledge indicates that this genus is probably more complex than previously thought, and its exact composition and systematic position will remain uncertain until the entire complex is reviewed.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Adams, H. and A. Adams. 1853. The genera of Recent Mollusca; arranged according to their organization. van Voorst, London, 1(1–8):256 p.

Cossmann, M. 1906. Essais de paléoconchologie comparée. F. R. de Rudeval, Paris, 7:261, 14 pls.

Cotton, B. C. 1959. South Australian Mollusca. Archaeogastropoda. W. L. Hawes, Adelaide, 449 p., 215 figs.

Fretter, V. 1951. Observations on the life histories and functional morphology of *Cerithiopsis tubercularis* (Montagu) and *Triphora perversa* (L.). Journal of the Marine Biological Association of Great Britain 29:567–586.

Golikov, A. N. and Y. I. Starobogatov. 1975. Systematics of prosobranch gastropods. Malacologia 15(1):185–227.

Iredale, T. 1936. Australian molluscan notes. No. 2. Records of the Australian Museum, Sydney 19:267–340, pls. 20–24.

Iredale, T. and D. F. McMichael. 1962. A reference list of the marine mollusca of New South Wales. The Australian Museum, Sydney, Memoir 11:109 p.

Kosuge, S. 1966. The family Triphoridae and its systematic position. Malacologia 4(2):297–324

Lea, H. C. 1845. Description of some new fossil shells, from the Tertiary of Petersburg, Va. Transactions of the American Philosophical Society, 2nd series 9:229–274 (1–48), pls. 34–37.

Marshall, B. A. 1977. The dextral triforid genus *Metaxia* (Mollusca: Gastropoda) in the south-west Pacific. New Zealand Journal of Zoology 4:111–117.

Marshall, B. A. 1978. Cerithiopsidae (Mollusca: Gastropoda)

of New Zealand, and a provisional classification of the family. New Zealand Journal of Zoology 5:47–120.

Marshall, B. A. 1980. The systematic position of *Triforis* Deshayes (Mollusca: Gastropoda). New Zealand Journal of Zoology 7:85–88.

Philippi, R. A. 1845. Diagnosen einiger neuen Conchylien. Archiv fuer Naturgeschichte 11:50–71.

Powell, A. W. B. 1930. New species of New Zealand Mollusca from shallow-water dredgings. Transactions of the New Zealand Institute 60:532–543.

Powell, A. W. B. 1951. Antarctic and Subantarctic Mollusca: Pelecypoda and Gastropoda. Discovery Reports 26:47–196, pls. 5–10.

Sars, G. O. 1878. Bidrag til Kundskaben om Norges Artiske Fauna. 1. Mollusca Regionis Arcticae Norvegiae. Brogger, Christiana, 466 p., 18 pls.

Tate, R. 1894. Unrecorded genera of the older Tertiary fauna of Australia, including diagnoses of some new genera and species. Journal of the Royal Society of New South Wales 27:167–198, pls. 10–13.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde. Jena, 1(1):v + 376 p.

Watson, R. B. 1886. Report on the Scaphopoda and Gasteropoda collected by *H.M.S. Challenger* during the years 1873–76. *In:* Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76 15(42): 756 p., 53 pls.

Wenz, W. 1940. Gastropoda, 1: Allgemeiner Teil und Prosobranchia. *In:* Schindewolf, O. H. (ed.). Handbuch der Paläozoologie. Borntraeger, Berlin, 4:721–960.

A New Species of *Phyllonotus* (Muricidae: Muricinae) from Isla del Coco, Costa Rica

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ABSTRACT

Phyllonotus eversoni, a new species from Isla del Coco, Costa Rica, is described and compared to *P. regius* (Swainson, 1821) and *P. erythrostomus* (Swainson, 1831).

INTRODUCTION

Isla del Coco (also known as Cocos Island), Costa Rica, is a small uninhabited island situated approximately 600 km SSW of Puntarenas, Costa Rica, at 5°33′ latitude and 87°03′ longitude. Cocos Island and the numerous islets which surround it are situated on the Cocos Ridge, which lies about 1,800 m (1,000 fm) below sea level (Hertlein, 1963:221–223).

The marine molluscan fauna at Cocos Island has predominantly Eastern Pacific affinities and probably was transported to the island from the mainland by westwardly directed ocean currents (Hertlein, 1963:226–227). However, he listed five species with Indo-Pacific origin. Emerson and Old (1964:90–91) and Shasky (1983:144, 1986:3–5) have noted several more species with Indo-Pacific affinities collected at Cocos Island. Emerson (1967: 89) discusses this transport of Indo-Pacific mollusks across 3,000 miles of open sea and offers as explanation that dispersal may occur by means of the eastward flowing North Equatorial countercurrent during the free swimming veliger stage.

Montoya (1983:35, 39–40) listed four species of marine mollusks found only at Cocos Island. Stingley (1984:28) described *Oliva foxi* with the only known locality listed as Cocos Island.

For a complete bibliography of Cocos Island molluscan faunal studies, see Montoya (1983:325–353, 1984:33–44). A complete list of the marine mollusks found at Cocos Island is in preparation (M. Montoya and D. R. Shasky).

Family **Muricidae** Rafinesque
Subfamily **Muricinae** Rafinesque

Genus *Phyllonotus* Swainson, 1833

Type species: *Murex margaritensis* (Abbott, 1958), new name for *Murex imperialis* Swainson, 1831 (not *M. imperialis* Fischer de Waldheim, 1807) by subsequent designation.

Phyllonotus eversoni new species
(figures 1, 2)

Description: Shell broadly fusiform, pear-shaped; protoconch of undetermined number of whorls; eight postnuclear, convex whorls; spire moderately high; body whorl broadly ovate; suture deeply impressed within a channel; aperture ovate; anal sulcus forming a deep trough between body and apertural varix; inner lip closely adherent above, forming a moderately raised inductura below, seven small nodes on anterior portion of columella; outer lip strongly crenulate and erect; weakly perceptible spiral cords on body, ending in broad open spines at aperture; aperture lirate within; siphonal canal broad, moderately long, distal portion narrow and recurved; left margin of canal simple, right side of canal follows indentations and grooves; siphonal fasciole with two well-preserved distal portions of previous canals; pseudoumbilicus present at juncture of canal, siphonal fasciole and inductura; three spinose varices on body whorl, penultimate whorl and antepenultimate whorl; first four postnuclear whorls with strong axial ribs and little indication of varices; fifth, sixth, and seventh postnuclear whorls with gradually diminishing axial ribs but with a series of nodes present at intersection of axial and spiral sculpture; varices erect, with broad open spines in two axial parallel rows on leading side; eight primary spines on

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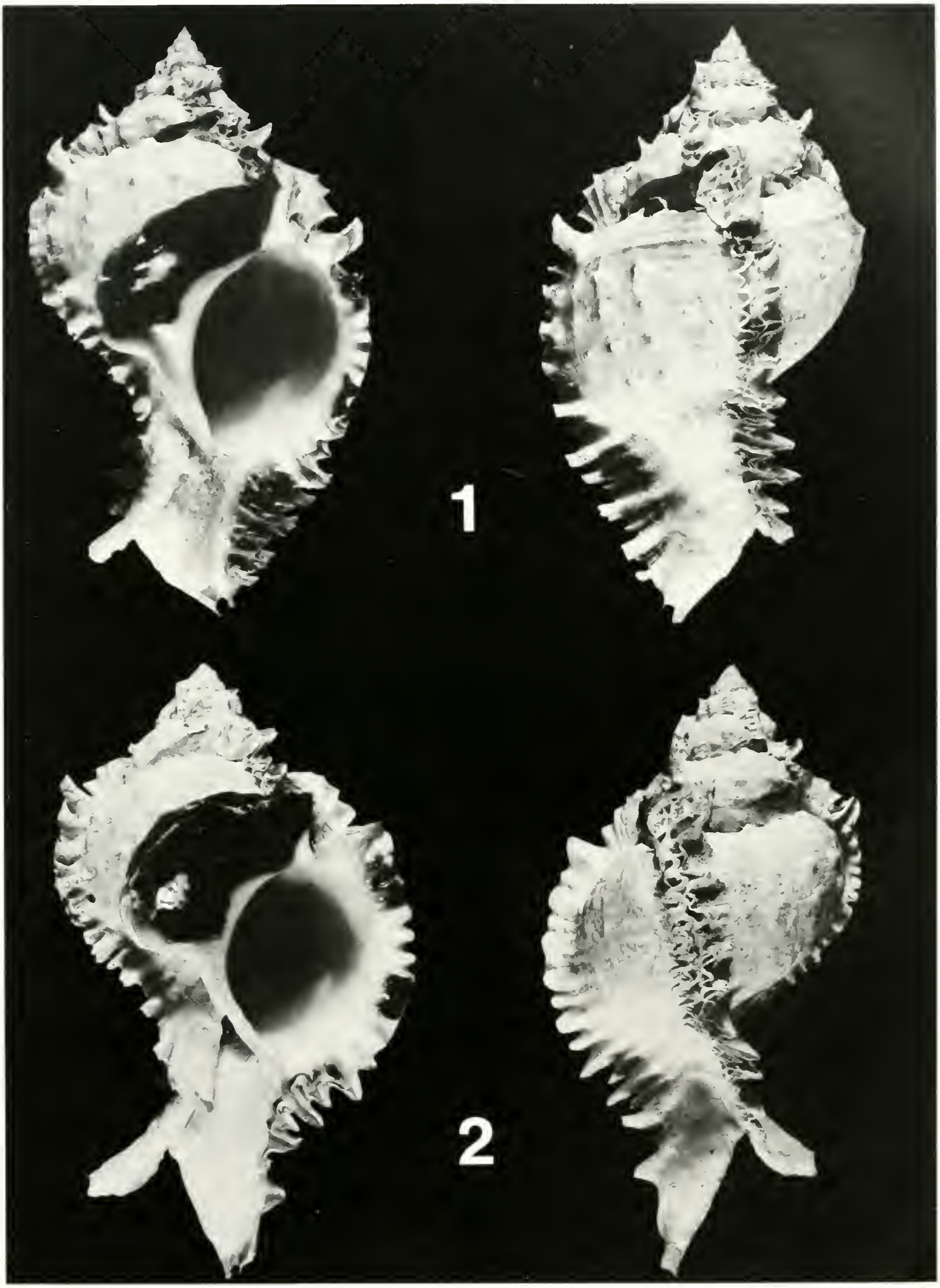
Figures 1, 2. *Phyllonotus eversoni* new species. 1. Holotype, USNM 859932, southwest side of Isla Manuelita, tangle net in 66 m, 143 mm long. 2. Paratype 1, USNM 859933, Chatham Bay, Cocos Island, tangle net in 66 m, 189 mm long.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body whorl and five on canal; buttresses extremely fine, thin walled, crossing the sutural channel and abutting the whorl above; five diffuse weak spiral cords on body whorl, four somewhat stronger cords on canal, entire dorsum rippled and crossed by microscopic spiral threads.

Color: Pale pink to deeper fleshy pink between varices, fading on canal; two to three weak brown bands on shoulder; leading sides of nodes on body whorl are brown; two brown spots on dorsal and ventral sides of the varices, one at shoulder and one at lower half of body whorl; some brown color on spines of canal; parietal callus lustrous brown above inductura, extending into anal sinus; a diagonal band of brown from previous parietal area preserved on last two whorls; columella deep pink.

Type locality: In 66 m, southwest side of Isla Manuelita, in tangle net. March 20, 1984.

Holotype: USNM 859932 (figure 1) 143 mm long × 77 mm wide.

Type material: Paratype 1: USNM 859933 (figure 2) 189 mm long × 104 mm wide. April 25, 1986. 66 m, Chatham Bay, Cocos Island, in tangle net. Paratype 2: SDNHM 91514 138 mm long × 81 mm wide. March 20, 1984. Roca Sucia in 27 m. Paratype 3: 170 mm long × 92 mm wide. March 20, 1984. East side of Isla Manuelita in 18 m. Collection of Gene Everson. Paratype 4: 128 mm long × 61 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of D. R. Shasky. Paratype 5: 130 mm long × 67 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of D. R. Shasky. Paratype 6: 151 mm long × 80 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of D. R. Shasky. Paratype 7: 166 mm long × 84 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of D. R. Shasky. Paratype 8: 103 mm long × 55 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Douglas von Kriegelstein. Paratype 9: 140 mm long × 75 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Douglas von Kriegelstein. Paratype 10: 144 mm long × 74 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Douglas von Kriegelstein. Paratype 11: 160 mm long × 85 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Partial specimen. Collection of Douglas von Kriegelstein. Paratype 12: 168 mm long × 82 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Douglas von Kriegelstein. Paratype 13: 134 mm long × 66 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Kirstie Kaiser. Paratype 14: 174 mm long × 87 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Kirstie Kaiser. Paratype 15: 137 mm long × 69 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Michel Montoya. Paratype 16: 151 mm long × 75 mm wide. April 26, 1987. 90 m Chatham Bay, Cocos Island. Collection of Michel Montoya.

Paratype 1, the largest specimen collected, is fully mature with a completely developed outer lip. This specimen has a long canal (80 mm compared to 44 mm on the holotype). There are 11 to 12 spiral cords on the body whorl which become evanescent in the intervarical areas, except on the canal. The outer lip on this large paratype is strongly reflexed, the crenulations terminating at right angle to the aperture; the anterior two-thirds portion has 24 short, strong, close-set lirae or denticles on the inner edge of the outer lip. The nodes on the columella numbering 10 in this specimen become stronger and elongate. The color of this specimen beneath a white opaque layer of soft calcium (intritacalx) is pale pink where the shell has been abraded. The parietal callus is a lustrous brown, the columella and inner side of aperture are pale pink.

The number of cords on the body whorl of this new species varies, as do the number of nodes on the columella, the length of the canal, and the number of spines on the varices. The reflected outer lip and the denticles on the inner lip vary with growth and maturity. Operculum is typically muricoid, unguiculate, and thickened marginally with a depressed central area on its inner surface, nucleus basal.

Etymology: We are pleased to name this species for Gene Everson who collected and donated the holotype and who has been generous in the past in contributing specimens for scientific study.

DISCUSSION

This new species is most closely related to *Phyllonotus regius* (Swainson, 1821) and *P. erythrostomus* from which it differs in the following characters: *P. regius* has six to seven varices, *P. erythrostomus* has four to five varices, while the new species has only three varices. The broad sutural channel found on the new species is lacking on both *P. regius* and *P. erythrostomus*.

D'Attilio (1984) has shown that occasional specimens of *P. erythrostomus* can have the same parietal and inductural coloring as *P. regius* and the new species.

Vokes (1984) figured this new species as *Chicoreus* (*Phyllonotus*) new species.

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LITERATURE CITED

Abbott, R. T. 1958. The marine mollusks of Grand Cayman Island, B.W.I. Academy Natural Sciences, Philadelphia, Monograph 11. 138 p., 5 pls.

D'Attilio, A. 1984. An unusual color form of *Phyllonotus erythrostomus* (Swainson, 1831). The Festivus 16(1):6–7, 4 figs.

Emerson, W. K. 1967. Indo-Pacific faunal elements in the Tropical Eastern Pacific, with special reference to the mollusks. Venus 25(3–4):85–93, 1 text fig.

Emerson, W. K. and W. E. Old, Jr. 1964. Additional records from Cocos Island. The Nautilus 77(3):90–93.

Hertlein, L. G. 1963. Contribution to the biogeography of Cocos Island, including a bibliography. Proceedings California Academy Sciences 4th Series 32(8):219–289, 4 figs.

Montoya, M. 1983. Los Moluscos Marinos de la Isla del Coco, Costa Rica. I. Lista Anotada de especies. Brenesia 21:325–353.

Montoya, M. 1984. Marine mollusks of Cocos Island, Costa Rica. I. Bibliographic compilation of species. Western Society of Malacology Annual Report (1983) 16:33–44.

Rafinesque, C. S. 1815. Analyse de la nature ou tableau du univers et des corps organises. Barravecchia, Palermo, p. 136–149.

Shasky, D. R. 1983. New records of Indo-Pacific Mollusca from Cocos Island, Costa Rica. The Nautilus 97(4):144–145.

Shasky, D. R. 1986. Update on mollusks with Indo-Pacific faunal affinities in the tropical eastern Pacific IV. The Festivus 18(1):3–5, 8 figs.

Stingley, D. V. 1984. A new *Oliva* from eastern Pacific (Gasteropoda [*sic*], Olividae). La Conchiglia 16(178–179):28.

Swainson, W. 1821. Exotic conchology, 1st ed., pt. 2, 7th pl. London, 39 p., 48 pls. (2nd ed., 1841, edited by Sylvanus Hanley, p. 5–6, pl. 15.)

Swainson, W. 1831. The zoological illustrations, Ser. 2, Vol. 3, p. 73, pl. 2. London. (Referenced in Sherborn as (2)II(16), 1831, pl. 73.)

Swainson, W. 1833. The zoological illustrations, Ser. 2, Vol. 3, p. 67, pl. 1 (not pl. 67, Vol. 2). (Referenced in both Naeve and Sherborn as 1833, Zoo. Illus. (2)3(22): pl. 100 Moll.)

Vokes, E. H. 1984. Comparison of the Muricidae of the eastern Pacific and western Atlantic with cognate species. Shells and Sea Life 16(11):210–215, 10 text figs., 2 pls.

A Revision of the Genus *Benthovoluta* with Notes on the Evolution of the Subfamily Ptychatractinae (Prosobranchia: Turbinellidae)

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ABSTRACT

The genus *Benthovoluta* Kuroda and Habe, 1950 is revised and restricted to four Recent species: *B. hilgendorfi* (von Martens, 1897); *B. gracilior* Rehder, 1967; *B. krigei* Kilburn, 1971; and *B. claydoni* new species. Phenetic analyses using morphometric data indicate that the three eastern Indian-western Pacific species are more closely related to each other than any is to the single species from the western Indian Ocean. Further phenetic analyses suggest that *Benthovoluta* is most closely related to the genus *Surculina* from off New Zealand and the eastern Pacific, that both are more remotely related to the small-shelled genera *Cyomesus*, *Metzgeria*, and *Ptychatractus*, all restricted to the Northern Hemisphere, and that the genera *Ceratoxancus* and *Latiromitra* are most distantly related, and may not belong to the family Turbinellidae. Dissections of *Benthovoluta claydoni* revealed that the mantle cavity and alimentary and male reproductive systems resemble those of the subfamily Turbinellinae, while the female reproductive system more closely resembled those of Vasinae and Columbariinae. A short, stout proboscis, as well as the presence of an amphipod carapace and lack of polychaete setae in the posterior alimentary canal, suggest a diet and mode of feeding that differ from those of other Turbinellidae. These dissections represent the first anatomical data for any species attributed to the subfamily Ptychatractinae. Cladistic analyses of anatomical characters reveal that the Ptychatractinae are most closely related to the Turbinellinae, and that the Vasinae are most distantly related to the other members of the family Turbinellidae.

INTRODUCTION

The genus *Benthovoluta* comprises a small, poorly known group of fusiform turbinellid gastropods that inhabit the bathyal zone along the margins of the Indian and Pacific oceans. Records are few, and the taxonomic position of the genus, as well as the often ephemeral inclusion of species within it, have been based on shell and occasionally on radular characters. Reports of fossil representatives are rare, tentative, and limited to Late Tertiary (Miocene or Pliocene) deep water deposits along the northwestern Pacific (Yokoyama, 1920; Taki & Oyama, 1954; MacNeil, 1960).

Kuroda and Habe (1950) erected the genus *Benthovoluta* within the family Volutidae, and designated *Phenacoptygma*? *kiiensis* Kuroda, 1931, a Recent species originally proposed with some doubt as a turrid, as type. These authors also included the Pliocene "*Mitra*" *plicifera* Yokoyama, 1920 (*non Mitra plicifera* S. V. Wood, 1848) in *Benthovoluta*, but placed both these taxa in the synonymy of *Voluta hilgendorfi* von Martens, 1897 in the same publication. On the basis of a figure of the radula of *B. hilgendorfi*, published without comment by Habe (1952), Kuroda (1965) transferred this genus to the family Turbinellidae and suggested affinities with the genera *Metzgeria* Norman, 1879 and *Ceratoxancus* Kuroda, 1952. Rehder (1967) noted similarities between the shell and radular morphologies of *Benthovoluta* and those of *Surculina* Dall, 1908, *Ptychatractus* Stimpson, 1865, and, more remotely, the fusiform species of *Turbinella* Lamarck, 1799. In the same paper, Rehder synonymized *Phenacoptygma* Dall, 1918 under *Surculina*.

Cernohorsky (1973) used Stimpson's (1865) family group name Ptychatractidae, previously placed in the synonymy of Turbinellidae by most authors, as a subfamily within Turbinellidae to include the five genera mentioned above. Quinn (1981) proposed the genus *Cyomesus* for a number of small-shelled species that had been referred to *Benthovoluta* by Cernohorsky (1973), and suggested that the Upper Cretaceous genera *Mesorhytis* Meek, 1876, *Paleofusimitra* Sohl, 1963, and *Mitrodomus* Sohl, 1963 as well as the Eocene genus *Fusimitra* Conrad, 1855 might also belong to the subfamily Ptychatractinae. Based on shell morphology, Bouchet and Waren (1985) referred the monotypic, eastern Atlantic, bathyabyssal genus *Latiromitra* Locard, 1897 to the family Turbinellidae, and considered *Cyomesus* a synonym.

Deep-water trawling off northwestern Australia by the Australian Commonwealth Scientific and Industrial Organization (CSIRO) as well as by commercial fishermen

has yielded a number of specimens, including several with preserved soft parts, of a new species of *Benthovoluta* that is described herein. This description includes the first account of the anatomy of any species attributed to the subfamily Ptychatractinae. The known species of *Benthovoluta* are reviewed and the phylogenetic affinities of this genus, and by inference the subfamily, are discussed.

MATERIALS AND METHODS

Specimens for anatomical studies were cracked in a vice, the loose shell fragments removed, and soft parts placed in 20% hydrochloric acid (HCl), to dissolve the remaining shell. Soft parts were rinsed in distilled water and returned to 70% ethanol for dissection.

Sections for analysis of shell ultrastructure were cut using a diamond saw. Some sections were broken to expose fracture surfaces, others polished and etched for a few seconds with 1% HCl. Radulae for SEM examination were critical point dried. In order to determine gut contents, the posterior esophagus, stomach, intestine, and rectum of three specimens of *Benthovoluta claydoni* were excised, transferred to a microscope slide, teased apart, and examined. Several drops of bleach (5% sodium hypochlorite, NaOCl) were then added to dissolve organic matter. After 20 minutes, the sample was diluted with distilled water, filtered through a 0.45 μm membrane filter, rinsed, dried, and examined under SEM. Scanning electron micrographs were taken using a Hitachi S-570 SEM.

The specimens of *Benthovoluta* listed in the material examined sections, as well as the published figure of the holotype of *B. krigei* (Kilburn, 1971: fig. 3a) were scored for the 12 characters listed in table 1. Analyses of relationships between species of *Benthovoluta* were confined to shell characters, as anatomical data were available for only one species, and published line drawings of the radulae of two other species lacked sufficient detail to ascertain differentiating characteristics. The mean values of the characters comprised the data matrix for phenetic analyses. To investigate the relationships between the Recent genera attributed to Ptychatractinae, specimens or figures of their type species (listed in table 2) were chosen to serve as exemplars, and scored for the characters listed in table 3. These values formed the data matrix used in a second series of phenetic analyses. Finally, the phylogenetic relationships between the four subfamilies of Turbinellidae were investigated using the taxa listed in table 4 as exemplars of their subfamilies, and scoring them for anatomical characters listed in table 5. Characters were polarized based on Ponder's (1973) analysis of the evolution of organ systems in Neogastropoda.

Morphometric shell characters [tables 1, 2 (characters 1–9)] were determined using CONCH version 1.0 (Chapman *et al.*, 1987). For phenetic analyses, the data were standardized (mean = 0, standard deviation = 1), a Euclidian distance matrix calculated, and phenograms based on UPGMA and single linkage (nearest neighbor) clustering algorithms produced using SYSTAT version 3.4 (Wilkinson, 1986). Cladistic analyses were run using PAUP version 2.4 (Swofford, 1985).

Table 1. Shell characters used in phenetic analyses of relationships between the species of *Benthovoluta*. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych, 1982).

1) Shape of the generating curve of the body cavity (Sbc)
2) Shape of the generating curve of the siphonal canal (Ssc)
3) Relative siphonal length (Rsl)
4) Siphonal angle (beta)
5) Angle of generating curve (theta)
6) Rate of whorl expansion (W)
7) Position of generating curve relative to axis (D)
8) Rate of whorl translation (T)
9) Aperture + siphonal canal length/shell length (A + SCL/SL)
10) Color pattern (CP): solid (0), banded (1)
11) Suture (Sut): adpressed (0), abutting (1)
12) Surface sculpture on body whorl (Sculp): incised spiral furrows (0), spiral cords (1), cancellate (2)

Repositories of examined specimens are indicated by the following abbreviations:

DMNH	Delaware Museum of Natural History
USNM	National Museum of Natural History, Smithsonian Institution
SAM	South African Museum
WAM	Western Australian Museum

SYSTEMATICS

Family **Turbinellidae** Swainson, 1840

This family is best known for its large, tropical, heavy-shelled, shallow-water species that comprise the low diversity subfamilies Turbinellinae and Vasinae. The bathyal subfamilies Columbariinae and Ptychatractinae are far more diverse and widely distributed, ranging from equatorial to polar latitudes. Species belonging to the latter two subfamilies tend to be significantly smaller and thinner-shelled. Characteristic features of the family include fusiform to biconical shells consisting of two or three layers of crossed-lamellar aragonite, bulbous protoconchs, open, axially-oriented siphonal canals, and columellae that usually have two to four spiral folds. Opercula are elongate and terminally nucleate. Animals generally have a long narrow proboscis, a small radular ribbon with tricuspid rachidian and mono- or bicuspid lateral teeth, an open or partially fused sperm groove, and lack accessory salivary glands. Diets consist mostly or exclusively of polychaetes (Hornell, 1914; Moses, 1923; Harasewych, 1983, 1986) sipunculids (Taylor *et al.*, 1980), and "worms" (Bandel, 1984).

Subfamily **Ptychatractinae** Stimpson, 1865

As taxa have been assigned to this, the most poorly known subfamily in Turbinellidae, exclusively on the basis of

Table 2. Recent genera attributed to the subfamily Ptychatractinae and their type species. Specimens or figures that provided characters for phenetic analyses are listed.

Benthovoluta Kuroda and Habe, 1950
Benthovoluta higendorfi (von Martens, 1897), USNM 824942, off Choshi, Japan (figure 1, herein; radula Rehder, 1967: fig. 11)

Ceratoxancus Kuroda, 1952
Ceratoxancus teremachii Kuroda, 1952, off Tosa, Japan (Shikama 1963: pl. 76, fig. 4; radula unknown)

Cyomesus Quinn, 1981
Cyomesus meckianus (Dall, 1889), lectotype, USNM 86970, BLAKE station 100, off Moro Light, Cuba 732 m (Quinn, 1981: fig. 1; radula Bayer, 1971: fig. 55D)

Latiromitra Locard, 1897
Latiromitra cryptodon (P. Fischer, 1882), MNHN, off Morocco, 1900 m (Bouchet & Waren, 1985: fig. 676; radula unknown)

Metzgeria Norman, 1879
Metzgeria albus (Jeffreys, 1873), INGOLF station 32, Davis Strait, western Greenland (Bouchet & Waren, 1985: fig. 677; radula fig. 393)

Ptychatractus Stimpson, 1865
Ptychatractus ligatus (Mighels and Adams, 1842), USNM 414668, off Eastport, Maine, in 18 m (unpublished photograph of shell; radula figure 19, herein)

Surculina Dall, 1908
Surculina blanda (Dall, 1980), holotype, USNM 123119, off Cocos Island, Gulf of Panama in 1951 m (Rehder, 1967: fig. 7; radula fig. 10).

Table 3. Shell and radular characters used in phenetic analyses of relationships between Recent genera attributed to the subfamily Ptychatractinae. Characters 1 through 8 describe the geometry of the generalized shell form (Harasewych, 1982).

1) Shape of the generating curve of the body cavity (Sbc)
2) Shape of the generating curve of the siphonal canal (Ssc)
3) Relative siphonal length (Rsl)
4) Siphonal angle (beta)
5) Angle of generating curve (theta)
6) Rate of whorl expansion (W)
7) Position of generating curve relative to axis (D)
8) Rate of whorl translation (T)
9) Aperture + siphonal canal length/shell length (A + SCL/SL)
10) Protoconch (Prot): multispiral (0); paucispiral (1)
11) Lateral radular teeth (Lat): single cusp emanating from outer edge of basal plate (0); base of single cusp spanning all or most of the basal plate (1)
12) Rachidian teeth with cusps spanning (Rach1): > 0.5 basal plate (0); < 0.5 basal plate (1)
13) Rachidian teeth with basal plate (Rach2): broad, curved (0); narrow, recurved (1)

shell and radular morphology, assumptions of monophyly for this group are, at best, tentative. Shells are fusiform, high-spired, and small (rarely exceeding 100 mm), with elongate, narrow apertures and zero to four, strong to weak columellar teeth. Radulae have tricuspid rachidian and monocuspid lateral teeth. Most members of this subfamily inhabit the bathyal zone, with some species occurring at depths in excess of 2,000 m. A number of the boreal species, including the type species of the type genus of the subfamily, have been taken in less than 20 m.

Genus *Benthovoluta* Kuroda and Habe, 1950

Benthovoluta Kuroda and Habe, 1950:37. Type species by original designation *Phenacoptygma? kiiensis* Kuroda, 1931; is *Voluta hilgendorfi* von Martens, 1897.

Although 10 Recent species, including one described herein, have been attributed to *Benthovoluta* (Shikama, 1971; Cernohorsky, 1973; Habe, 1976), this genus is here restricted to the four species discussed below. Characteristic features of the genus include comparatively large shells with long siphonal canals, rachidian teeth with cusps limited to the central half of the tooth, and broad-based, trowel-like lateral teeth. The remaining species are referred to the genus *Cyomesus* Quinn, 1981, which may be readily distinguished from *Benthovoluta* on the basis of its much smaller shell, with shorter siphonal canal and proportionally higher spire, and a radular ribbon in which the rachidian teeth are stouter, with larger, broader cusps, and lateral teeth that are narrow, long, and scythe-shaped.

Benthovoluta hilgendorfi (von Martens, 1897) (figures 1–3)

Voluta hilgendorfi von Martens, 1897:176, pl. 17, fig. 1.
?*Mitra plicifera* Yokoyama, 1920:48, pl. 2, figs. 16a,b; Hatai and Nishiyama, 1952:215; Taki and Oyama, 1954: pl. 3, figs. 16a,b; Cernohorsky, 1972:223 (*non Mitra plicifera* S. V. Wood, 1848).
Phenacoptygma ? kiiense Kuroda, 1931:48, fig. 1
Benthovoluta hilgendorfi (von Martens) Kuroda and Habe, 1950:37, pl. 5, fig. 2, Kira, 1962:92, pl. 33, fig. 3; Shikama, 1963:97, pl. 79, fig. 7; Kuroda, 1965:50; Cernohorsky, 1973: 126–127 (in part).

Description: Shell (figures 1, 2) to 84 mm, solid, elongate, fusiform. Protoconch (figure 3) of ¾ whorl, smooth, deflected from coiling axis. Transition to teleoconch abrupt, marked by thickened protoconch lip and first appearance of spiral threads and axial ribs. Teleoconch with up to 10 convex, rounded whorls. Suture adpressed. Shoulder rounded. Spiral sculpture of incised spiral lines, 37–45 on body whorl, 9–11 on exposed portions of previous whorls, and 20–27 on siphonal canal. Incised lines may be thinner and shallower along siphonal canal. Axial sculpture of 12–14 costae, prominent on early whorls, rarely occurring beyond 8th postnuclear whorl. Aperture elongate, elliptical. Outer lip smooth, thin, porcellaneous. Inner lip smooth, glazed. Columella solid, with 3 (oc-

Table 4. Species and specimens that provided anatomical data for cladistic analyses of relationships between the subfamilies of Turbinellidae.

Columbariinae Tomlin, 1928
- *Coluzea rotunda* (Barnard, 1959), 2 ♀, 2 ♂, SAM A 4592, off Cape Town, South Africa, 1,006–869 m

Ptychatractinae Stimpson, 1865
- *Benthovoluta claydoni* new species, data contained herein

Turbinellinae Swainson, 1840
- *Turbinella angulata* (Lightfoot, 1786), 2 ♀, 2 ♂, USNM 846315, off Carrie Bow Cay, Belize, 1–2 m

Vasinae H. and A. Adams, 1853
- *Vasum muricatum* (Born, 1778), 2 ♀, 2 ♂, USNM 846316, off Carrie Bow Cay, Belize, 1–2 m

Table 5. Characters and character states used in cladistic analyses of the relationships between the subfamiles of Turbinellidae.

1) Siphon, long, exposed (a); narrow, covered (b); broad, fleshy, covered (c)
2) Median cephalic furrow, absent (a); present (b)
3) Retracted proboscis: linear (a); folded (b)
4) Proboscis retractor muscles: paired (a); single (b)
5) Lateral radular teeth: bicusped (a); monocusped (b)
6) Rachidian teeth with cusps spanning: > 0.75 basal plate (a); < 0.75 basal plate (b)
7) Anal gland, present (a); absent (b)
8) Bursa copulatrix: present (a); absent (b)
9) Sperm groove: along inner lateral edge of penis (a); runs ventrally just prior to opening (b)
10) Penial papilla: absent (a); present (b)

casionally 4) simple folds. Central fold most prominent, may become fused with anteriormost fold. Siphonal canal broad, tapers distally, crosses coiling axis. Interior shell surfaces smooth, except for columellar folds. Color chestnut brown. Early whorls may be lighter. Aperture may have a whitish overglaze. Operculum reduced, thin, elongate, with terminal nucleus. Soft parts other than radula are unknown. The radula was figured by Habe (1952) and refigured by Rehder (1967).

Type locality: Von Martens (1897:176) gave the locality as "Japan, probably from Hakodate, Hilgendorf". This is outside the range of the species, as reported by several Japanese authors (*e.g.*, Kira, 1962:92; Kuroda *et al.*, 1971: 199), and probably in error.

Material examined: USNM 605772, Tosa, Japan, 274 m; USNM 612610, Japan; USNM 824942, off Choshi, Japan.

Distribution: Off the eastern coast of Japan, south of Choshi (Central Honshu), in 50–300 m.

Ecology: This species inhabits sandy bottoms at depths of 50–300 m. Most specimens examined had one or more repaired breaks, indicating unsuccessful predation by crabs and/or fish.

Remarks: This species is readily identified on the basis of its chestnut brown color and its spiral sculpture of incised furrows.

Benthovoluta gracilior Rehder, 1967
(figures 4–6)

Benthovoluta gracilior Rehder, 1967:185, figs. 5, 6; Cernohorsky, 1973:129.

Description: Shell (figures 4, 5) to 57 mm, thin, biconical, narrowly fusiform. Protoconch (figure 6) of ¾ whorl, smooth. Transition to teleoconch demarcated by abrupt appearance of axial costae and spiral threads. Teleoconch with up to 10¾ whorls. Suture adpressed. Shoulder pronounced, rounded. Spiral sculpture of 42–46 fine cords on body whorl, 48–52 on siphonal canal, and 16–18 on exposed portions of earlier whorls. Fine spiral threads may occur between adjacent cords, especially between shoulder and suture. Axial sculpture of 16–18 prominent costae per whorl. Axial costae poorly defined below midpoint of body whorl. Aperture elongate, narrow. Outer lip thin, smooth. Columella solid, with 2 folds, posterior fold more prominent. Siphonal canal long, narrow, crosses coiling axis. Periostracum thin, of straw-colored axial blades. Operculum and soft parts unknown.

Type locality: Off Cagayan Islands, north Sulu Sea, Philippines, 9°38′30″N, 121°11′E, in 929 m. "Albatross I" sta. 5423.

Material examined: USNM 637252 (holotype), USNM 238408 (4 paratypes), DMNH 15456 (paratype), all from the type locality.

Distribution: Known only from the type locality.

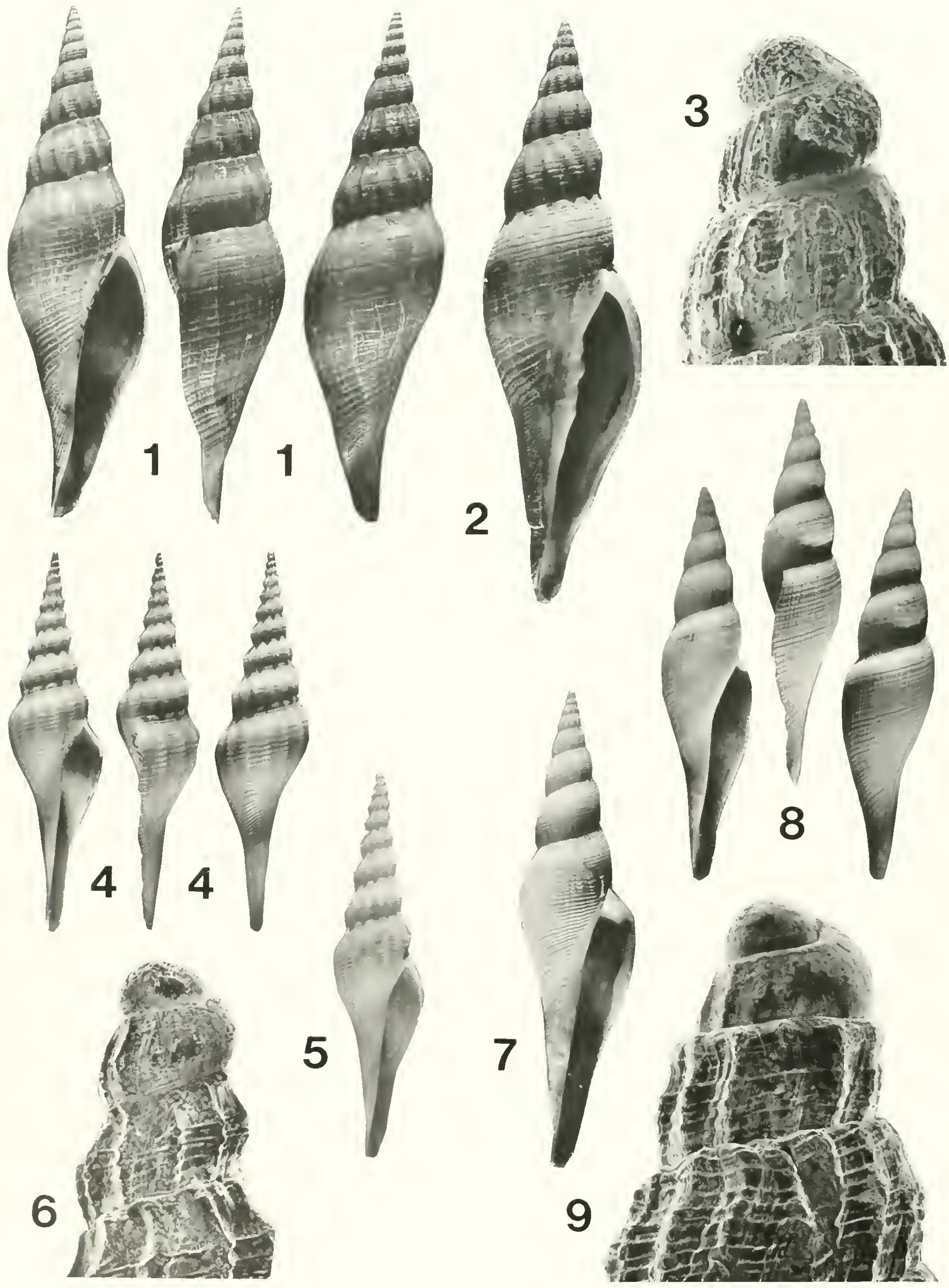
Ecology: This species was taken in 929 m on gray mud and coral sand bottom.

Remarks: This species differs from its congeners in having a smaller, thinner, more highly spired shell, with axial ribs that are prominent on the body whorl. It has only been taken once, and at twice the depth inhabited by its known congeners.

Benthovoluta krigei Kilburn, 1971
(figures 7–9)

Benthovoluta krigei Kilburn, 1971:127–130, figs. 2d, 3a,b; Kensley, 1973:180, fig. 686.

Description: Shell (figures 7, 8) to 71 mm, solid, inflated, narrowly fusiform. Protoconch (figure 9) of ¾ whorl, smooth, globose, deviated from coiling axis. Transition to teleoconch marked by abrupt appearance of numerous fine spiral threads and strong axial ribs. Teleoconch with up to 9⅔ convex, rounded whorls. Suture strongly adpressed in early whorls, whorls abutting in larger specimens. Shoulder weak, rounded. Spiral sculpture of broad,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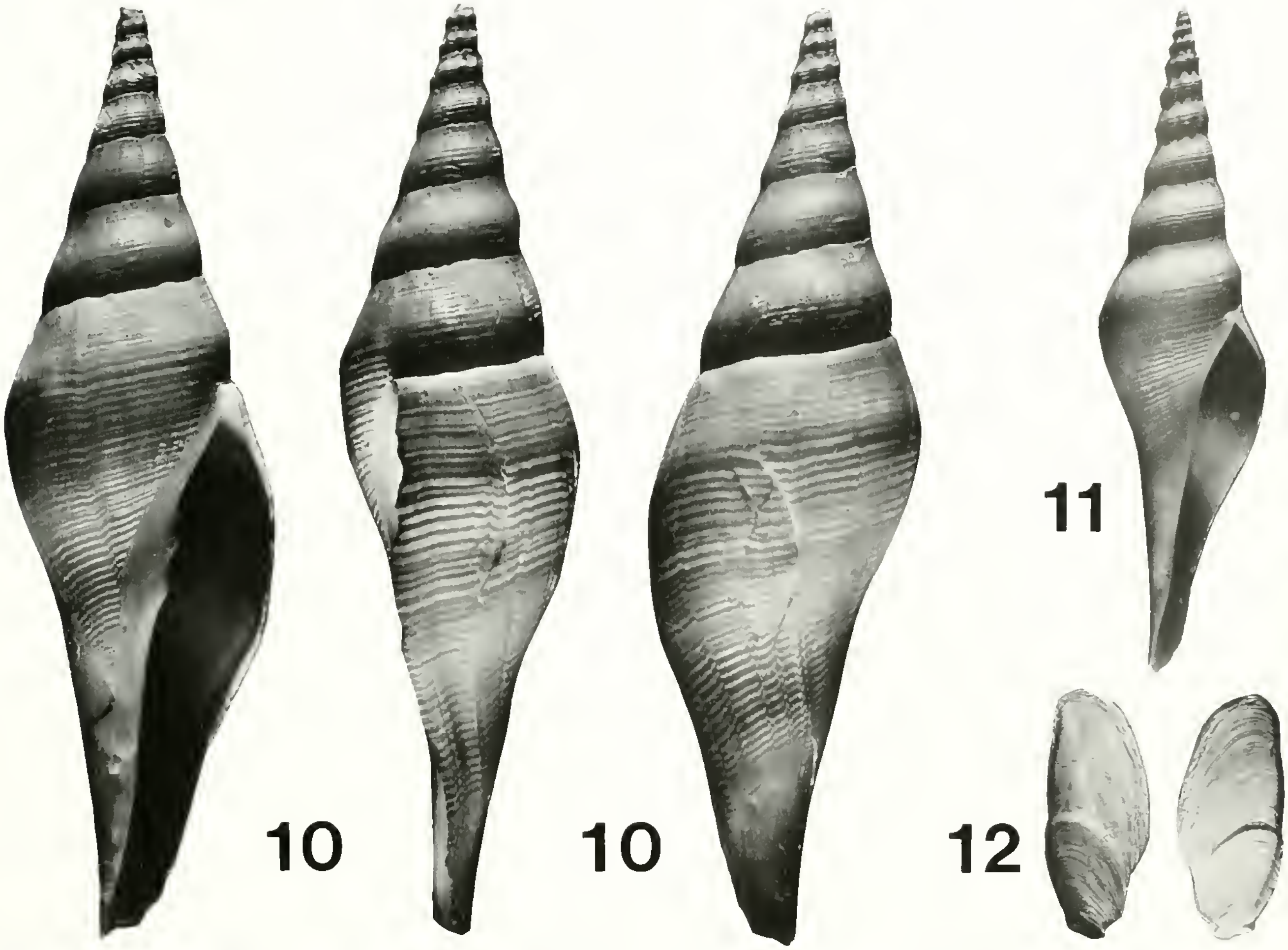


Figures 1–3. *Benthovoluta hilgendorfi* (von Martens, 1897). **1.** USNM 824942, off Choshi, Japan. **2.** USNM 605772, Tosa, Japan, in 274 m. **3.** Protoconch of specimen in figure 1. **Figures 4–6.** *Benthovoluta gracilior* Rehder, 1967. **4.** Holotype, USNM 637252. **5.** Paratype, USNM 238408, both from off Cagayan Islands, northern Sulu Sea, Philippines, in 928 m. **6.** Protoconch of specimen in figure 5. **Figures 7–9.** *Benthovoluta krigei* Kilburn, 1971. **7, 8.** USNM 824943, off Inhaca Island, Mocambique, trawled in 475 m. **9.** Protoconch of specimen in figure 7.

Figures 10–12. *Benthovoluta claydoni* new species. **10.** Holotype, WAM 3252-83. **11.** Paratype 1, USNM 862217, both from SW of Imperieuse Reef, Rowley Shoals, Western Australia, 400–401 m. **12.** Operculum of holotype, left—inner surface, right—outer surface. All shells 1.25 ×, protoconchs 30.0 ×, operculum 3.0 ×.

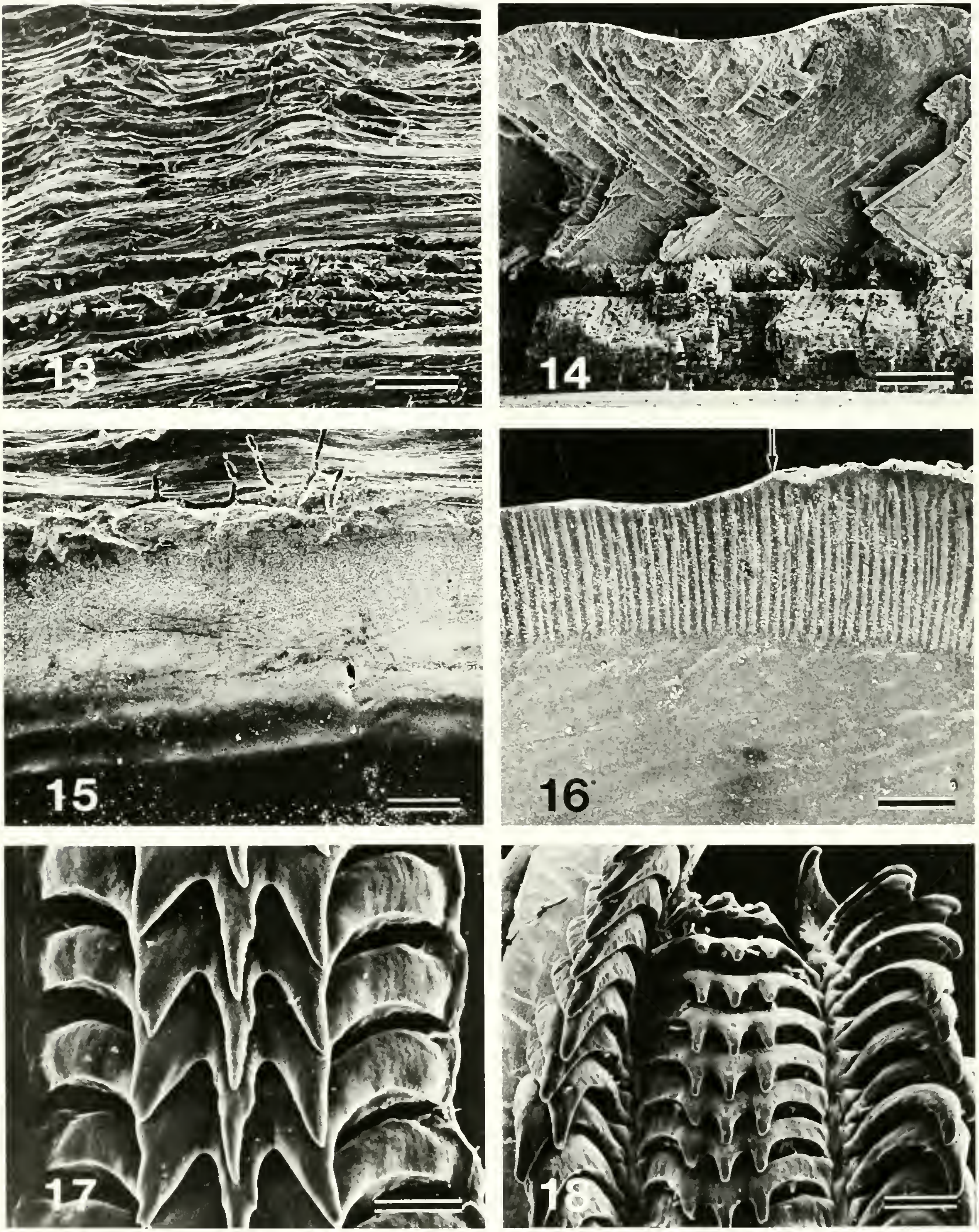
rounded, closely-spaced cords that give shell surface a deeply incised appearance, 36–48 on body whorl, 20–23 on penultimate whorl, 13–19 on siphonal canal. Axial sculpture of 12–16 costae, prominent on early whorls, becoming reduced and generally absent by 6th postnuclear whorl. Aperture elongate, narrow. Outer lip thin, strongly sinuate posteriorly. Inner lip smooth, with shell surface dissolved to below level of spiral sculpture. Columella solid, folds weak or lacking. Siphonal canal long, broad, distally tapering. Interior shell surfaces smooth. Color light tan, with darker brown between suture and shoulder, along the anterior half of the body whorl, distal portion of the siphonal canal, and in a thin band along the margin of the outer lip. Periostracum unknown. Operculum as in *B. hilgendorfi* (*fide* Kilburn, 1971). Kilburn (1971:129) described the animal as white, with thin, filiform tentacles with eyes at the outer sides of their bases. Radula (Kilburn, 1971:129, fig. 2d) with 69 rows of teeth. Rachidian teeth tricuspid, with broad, arcuate base. Lateral teeth monocuspid, claw-like.

Type locality: 80 km due east of Inhaca Island, Mocambique, in 512 m (280 fm).

Material examined: USNM 824943, off Inhaca Island, Mocambique, in 475 m.

Distribution: This species has only been taken off Inhaca Island, Mocambique at depths of 475–512 m.

Remarks: Kilburn (1971:129) considered this species to more closely resemble *Surculina* than any species of *Ben-*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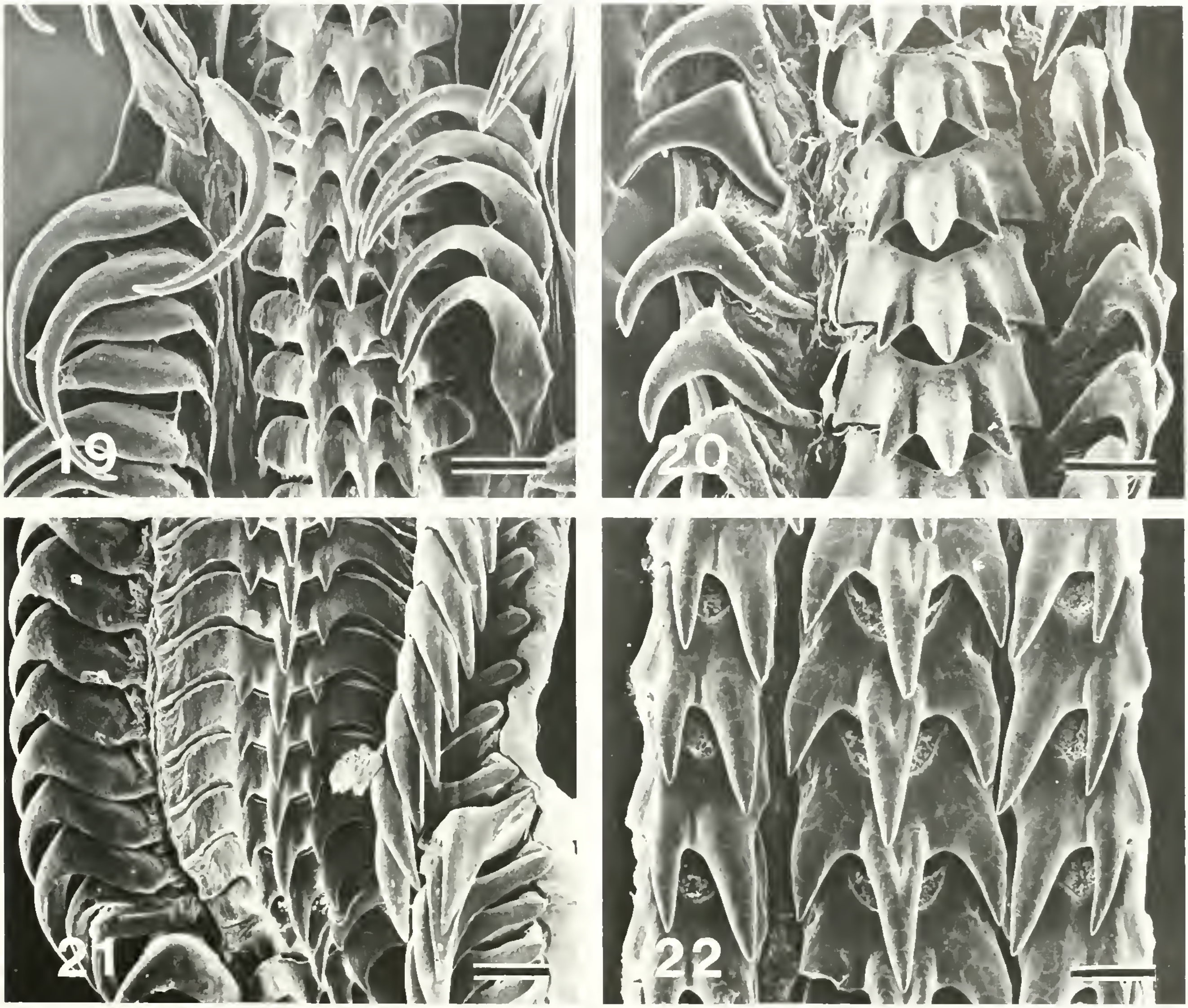


Figures 13–18. *Benthovoluta claydoni* new species. **13.** Periostracum, scale bar = 300 μm. **14.** Shell ultrastructure, fracture surface parallel to growing edge, scale bar = 200 μm. **15.** Parietal area of columella, showing reabsorption of portion of outermost shell layer, scale bar = 100 μm. **16.** Section through columella perpendicular to shell axis, surface polished and acid-etched (1% HCl). Arrow indicates limit of shell reabsorption, scale bar = 200 μm. **17.** Rachidian teeth, scale bar = 30 μm. **18.** Radular ribbon, scale bar = 50 μm.

Figure 19. Radular ribbon of *Ptychatractus ligatus* (Mighels and Adams, 1842), scale bar = 30 μm. **Figure 20.** Radular ribbon of *Cyomesus chaunax* (Bayer, 1971), scale bar = 20 μm. **Figure 21.** Radular ribbon of *Turbinella pyrum* (Linné, 1758), scale bar = 30 μm. **Figure 22.** Radular ribbon of *Vasum muricatum* (Born, 1778), scale bar = 50 μm.

thovoluta in shell morphology, but assigned it to the latter genus because Dall (1908:292) reported that *Surculina cortezi* (Dall, 1908) lacked eyes, tentacles, and operculum, and due to a misinterpretation of Rehder's (1967: fig. 10) figure showing two views of a monocuspid lateral tooth as a bicuspid lateral tooth. Although the relationship between *Benthovoluta* and *Surculina* bears closer investigation when anatomical material becomes available, *Benthovoluta krigei* is more closely related to its Indo-Pacific congeners than to any species of *Surculina*. Examination of additional specimens of *B. krigei* revealed that several had weak but nevertheless distinguishable columellar folds corresponding to the anteriormost two folds of *B. hilgendorfi*.

Benthovoluta claydoni new species
(figures 10–18, 23–26; table 6)

Description: Shell (figures 10, 11) to 101 mm, solid, elongate, fusiform. Protoconch broken or abraded on all

Table 6. *Benthovoluta claydoni* new species. Measurements of shell characters. Linear measurements in mm

Character	$\bar{x}$	Range	SD
Shell length (SL)	85.0	62.2–100.9	9.4
Aperture + siphonal canal length (A + SCL)	51.0	35.2–60.3	6.6
A + SCL/SL	0.599	0.566–0.622	0.018
# Whorls	10.3	8–13	1.4
Spire angle	29.1	25.5–32.0	2.4

specimens examined. Teleoconch with up to 13 slightly convex whorls. Suture adpressed. Shoulder somewhat pronounced on early whorls, becoming more rounded with increasing size. Spiral sculpture of weak, simple cords, 33–42 on body whorl, 12–18 on exposed portions of earlier whorls, 15–35 on siphonal canal. Cords strongest between shoulder and siphonal canal, weakest at suture and distal portion of siphonal canal. Axial sculpture of 9–11 costae, most pronounced on earlier whorls, becoming reduced and usually absent by 7th postnuclear whorl. Aperture elongate, elliptical. Outer lip smooth, thin, porcellaneous. Inner lip smooth, characterized by dissolution of portion of outermost shell layer from parietal region (figures 15, 16). Columella solid, with 3 simple folds, central fold most prominent, posteriormost fold weakest and sometimes absent. Siphonal canal broad, long, crosses coiling axis. Interior shell surfaces uniformly smooth, unmodified except by columellar folds. Periostracum (figure 13) of short, thin, straw-colored, axial blades. Operculum (figure 12) greatly reduced ($< 0.4 \times$ aperture length), thin, elongate, terminally nucleated.

Ultrastructure: Shell of two orthogonal layers of crossed-lamellar aragonite (figure 14). Outer layer, 420–620 μm thick, with crystal faces colabrally aligned. Inner layer, 320–350 μm thick, with crystal faces perpendicular to growing edge. Spiral sculpture limited to outer layer, columellar folds comprised of inner layer. Portion of outer layer along parietal area dissolved to below level of spiral sculpture (figures 15, 16), indicating boundary of inner lip.

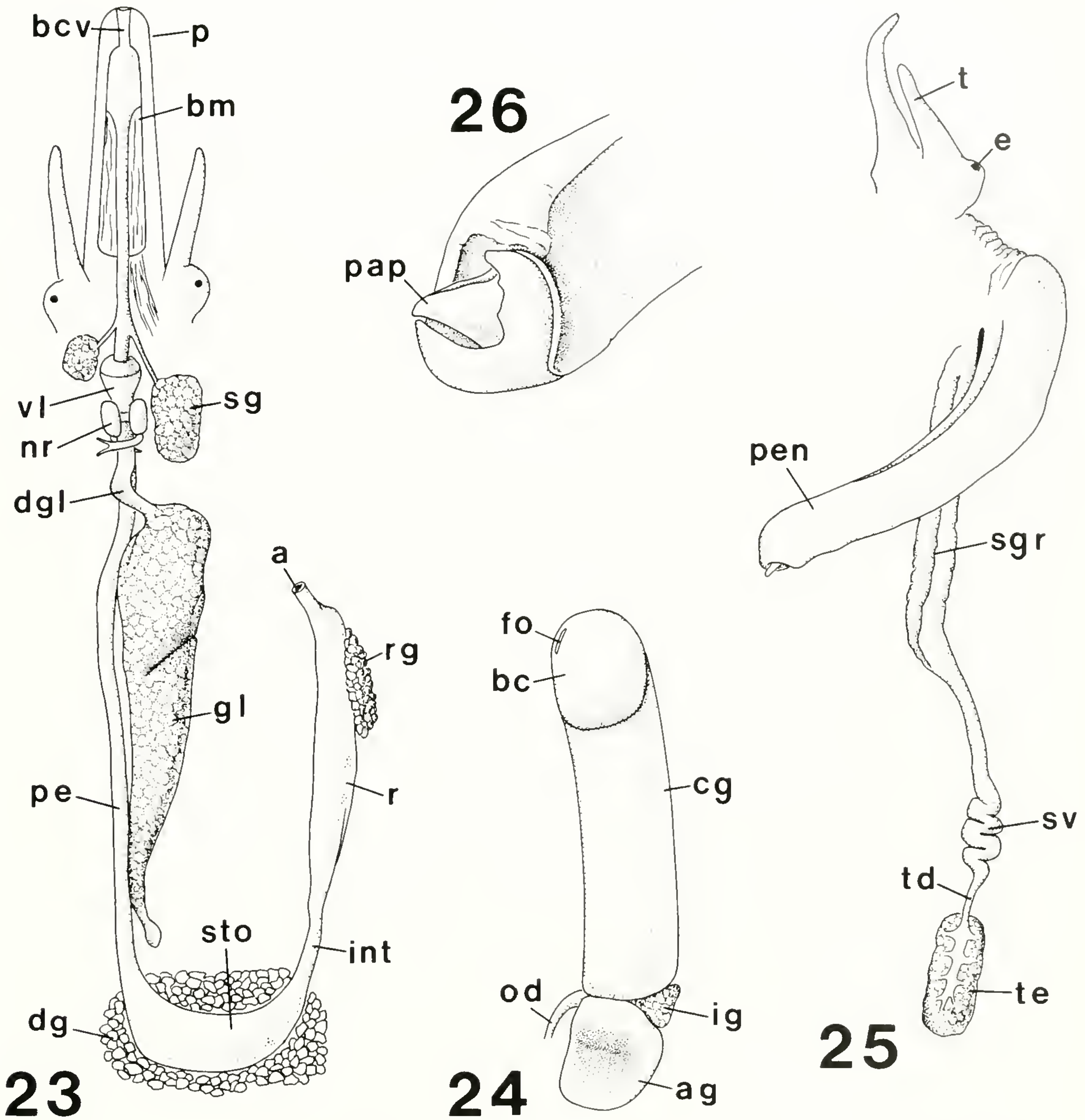
External anatomy: Soft parts comprise 4½ whorls. Mantle cavity extends over 1 whorl, kidney spans ½ whorl, digestive gland 2½ whorls. Foot short, narrow (L/W = 2.0), squarish anteriorly, rounded posteriorly. Operculum as broad as foot. Preserved animals khaki tan in color, lack discernible color pattern. Siphon broad, muscular, simple. Head small, narrow, with long tentacles (figure 25, t) that have large, black eyes (figure 25, e) at their outer bases.

Mantle cavity: Mantle cavity organs similar to those of *Fulgurofusus brayi* (Clench, 1959), as described by Harasewych (1983). Mantle edge slightly thickened, finely papillose. Osphradium large, long (L/W = 4.3), consisting of about 70 triangular filaments above and 60 below the axis. Ctenidium of about 200 deep hanging leaflets, 1.9 × as long and 1.0 × as wide as osphradium. Hypobranchial gland transversely pleated, deeply glandular, unpigmented. Rectum and genital ducts along right side of mantle cavity, large pericardium and kidney along its back wall.

Alimentary system: Rhynchostome opens at base of tentacles, leads to short, muscular, pleurembolic proboscis (figure 23, p). Single, large proboscis retractor muscle attaches to right wall of cephalic hemocoel and surrounds a large blood vessel. Buccal cavity (figure 23, bcv) deep, with strong longitudinal folds, lacks jaws. Buccal mass (figure 23, bm) large, muscular, projects beyond rear of retracted proboscis. Radular sack short, contained within buccal mass. Radular ribbon (figure 18) short (4 mm), narrow (300 μm), contains 88–97 rows of teeth (n = 3). Rachidian teeth (figure 17) with three cusps emanating from middle half of tooth. Basal plate recurved, narrow. Lateral teeth with single, trowel-like cusp. Esophagus runs anteriorly from rear of proboscis, expanding to form large valve of Leiblein (figure 23, vl) before passing through nerve ring. Salivary glands (figure 23, sg) asymmetrical, situated at rear of retracted proboscis. Ducts from salivary glands join esophagus just anterior to the valve of Leiblein, become embedded beneath the dorsal folds. Accessory salivary glands absent. Between nerve ring and duct from gland of Leiblein (figure 23, dgl), esophagus expands and becomes glandular, resembling a "glande framboisee" (Fretter & Graham, 1962:216). Gland of Leiblein (figure 23, gl) large, brownish, broad anteriorly, tapering posteriorly to form blind ampulla, fills posterior half of cephalic hemocoel. Posterior esophagus (figure 23, pe) runs along left side of gland of Leiblein, expanding along anterior face of digestive gland (figure 23, dg) to form stomach. Stomach (figure 23, sto) U-shaped, with small caecum, prominent typhlosoles. Duct from digestive gland enters near esophageal opening. Intestine (figure 23, int) short. Rectum (figure 23, r) broad, thin-walled, voluminous. Rectal gland (figure 23, rg) spans dorsal, distal ¼ of rectum. Anus (figure 23, a) simple, pendant from wall of mantle cavity.

Female reproductive system: Ovary salmon colored, ascinous, lines adapical side of digestive gland. Oviduct (figure 24, od) thin, passes through kidney, runs along pericardial wall before joining pallial oviduct at juncture of albumen gland, capsule gland, and duct of ingesting gland. Albumen gland (figure 24, ag) short, laterally compressed, forms anterior portion of right wall of kidney. Ingesting gland (figure 24, ig) small, whitish, with long duct. Capsule gland (figure 24, cg) long, narrow, divided into proximal and distal regions by transverse ridge visible along outer wall as narrow, light colored band. Bursa copulatrix (figure 24, bc) ovate, abutts against capsule gland, laterally compressing its anterior end. Female opening (figure 24, fo) ventral slit along anteriormost end of bursa copulatrix.

Male reproductive system: Testis (figure 25, te) pale orange, situated along adapical side of digestive gland. Testicular duct (figure 25, td) runs anteriorly, expands and becomes convoluted, forming seminal vesicle (figure



Figures 23–26. Anatomical features of *Benthovoluta claydoni* new species. **23.** Alimentary system. **24.** Female pallial oviduct. **25.** Male reproductive system. **26.** Ventral view of penis tip.

a, anus; ag, albumen gland; bc, bursa copulatrix; bcv, buccal cavity; cg, capsule gland; dg, digestive gland; dgl, duct of gland of Leiblein; e, eye; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; int, intestine; od, oviduct; p, proboscis; pe, posterior esophagus; pen, penis; r, rectum; rg, rectal gland; sg, salivary gland; sgr, sperm groove; sto, stomach; sv, seminal vesicle; t, tentacle; td, testicular duct; te, testis; vl, valve of Leiblein.

25, sv) along anterior portion of kidney and pericardium. Duct straightens, enters rear of mantle cavity and runs anteriorly along its wall, ventral to rectum, descending to floor of mantle cavity at midlength to form muscular, open groove (figure 25, sgr). Groove runs anteriorly to base of long, dorsoventrally compressed, distally tapering penis (figure 25, pen), and along its inner lateral edge to the distal end, where it passes along the ventral surface and extends to tip of papilla (figure 26, pap), situated in a concavity at the outer distal edge of penis.

Kidney: Kidney large, with broad nephridial gland adjacent to pericardium and about 10 heavily pleated lamellae emanating from dorsal and lateral walls.

Etymology: This species honors Michael Claydon, of Port Hedland, Western Australia, who first brought it to my attention, and generously provided material for study.

Type locality: SW of Imperieuse Reef, Rowley Shoals, Western Australia, 18°05′S, 118°10′E, in 400–401 m, mud bottom.

Holotype: Western Australian Museum WAM 3252-83, ♂, length 84.7 mm.

Paratypes: Paratypes 1–2, National Museum of Natural History, Smithsonian Institution USNM 862217, paratypes 3–4, WAM 3252-83, all from the type locality; paratype 5, WAM 972-84, WNW of Lacepede Archipelago, Western Australia, 15°40.2′S, 120°37.3′E to 15°42.6′S, 120°34.6′E, in 500–504 m, soft bottom; paratype 6, WAM 977-84, W of Cape Leveque, Western Australia, 16°09.5′S, 120°08.8′E to 16°07.6′S, 120°10.0′E, in 600–596 m, soft bottom; paratype 7, WAM 990-84, W of Broome, Western Australia, 17°59′S, 118°11′E to 18°01′S, 118°08′E, in 530–560 m, soft bottom; paratype 8, WAM 1556–84, WNW of Lacepede Archipelago, Western Australia, 15°46.4′S, 120°39.9′E to 15°43.8′S, 120°39.8′E, in 446–450 m, soft bottom; paratype 9, WAM 1564-84, WNW of Lacepede Archipelago, Western Australia, 15°51.2′S, 120°44.3′E to 15°49.3′S, 120°45.3′E, in 350–348 m, soft bottom; paratype 10, WAM 1866-84, W of Lacepede Archipelago, 16°55.4′S, 119°52.3′E to 16°57.4′S, 119°46.4′E, in 436–448 m, soft bottom; paratypes 11–12, WAM 1908-84, W of Lacepede Archipelago, Western Australia, 16°57.4′S, 119°52′E to 16°55′S, 119°56′E, in 434–432 m, soft bottom; paratype 13, WAM 1160-85, W of Lacepede Archipelago, Western Australia, 16°55.2′S, 119°50.9′E to 16°56.3′S, 119°54.8′E, in 430–436 m, soft bottom; paratype 14, USNM 862218, NW of York Sound, Western Australia, 12°54.4′S, 123°00.2′E to 12°50.6′S, 123°00.4′E, in 452–462 m, soft bottom; paratype 15, WAM 1681-84, NW of Collier Bay, Western Australia, 13°44′S, 122°13.3′E to 13°22.3′S, 122°14.7′E, in 496–494 m, soft bottom; paratypes 16–17, USNM 845602, 30–60 miles SW of West Island, Rowley Shoals, Western Australia, 250–430 m; paratype 18, American Museum of Natural History, AMNH 221361, off Port Hedland, Western Australia, in 450 m.

Distribution: All specimens examined in this study were taken along the upper continental slope off northern Western Australia at depths of from 350 to 596 m. The mean station depth was 453 m (n = 15). Cernohorsky (1973) figured and described a single, male specimen of this new species [as *Benthovoluta hilgendorfi* (von Martens, 1897)] from the Celebes Sea, 25 miles east of Zamboanga, Philippines, in about 450 m.

Ecology: *Benthovoluta claydoni* occurs on mud and soft bottoms at depths from 350 to 596 m. Live collected specimens had a thin or worn periostracum, yet lacked epizoans, suggesting that this species may be an infaunal burrower. Numerous repaired breaks in a majority of the specimens examined, indicate frequent, unsuccessful predation by crabs and/or fish. Contents of the alimentary systems of three individuals were examined, one stomach contained fragments of an amphipod carapace. No polychaete setae were found in the guts of any of these specimens.

Comparative remarks: *Benthovoluta claydoni* most closely resembles the Japonic *B. hilgendorfi* (von Martens, 1897), which can be distinguished from *B. claydoni* by its chestnut brown color, spiral sculpture of incised furrows, and more pronounced axial sculpture. *Benthovoluta krigei* has a narrower, more fusiform shell with more evenly convex whorls, weaker axial sculpture that gives the body whorl a finely cancellate appearance, is tan in color with two to three darker spiral bands, and lacks or has very weak columellar folds. *Benthovoluta gracilior* Rehder, 1967, from somewhat deeper waters 928 m) of the Sulu Sea, differs from this new species in being smaller and more fusiform, and in having stronger axial sculpture that is not limited to the early whorls.

DISCUSSION

The genus *Benthovoluta*, as restricted above, is limited to the continental slopes along the margins of the Indian and western Pacific oceans in the Recent fauna. Fossil records are limited to the Pliocene of Japan (Yokoyama, 1920; Taki & Oyama, 1954) and the late Miocene or early Pliocene of Okinawa (MacNeil, 1960), and are all from bathyneritic or bathyal depths. Of the Okinawan fossil species, *Benthovoluta okinavensis* MacNeil, 1960 is here reassigned to the genus *Cyomesus* on the basis of its small size, short siphonal canal, absence of spiral sculpture, prominent axial ribs, and overall resemblance to *Cyomesus barthelowi* (Bartsch, 1942). However, the fragments illustrated as *Phenacoptygma* new species (MacNeil, 1960: pl. 9, figs. 4, 5), are referable to the genus *Benthovoluta*, and represent the oldest known record for the genus.

Phenetically deduced relationships between the species of *Benthovoluta* based on UPGMA and single linkage clustering using the data in table 7 are shown in figure 27. Both algorithms produced dendrograms with identical topologies. Closest relationships are between the eastern Indian-western Pacific species, which differ in geographic and (*B. hilgendorfi-B. claydoni*)/or (*B. claydoni-B. gracilior*) bathymetric distributions. Several examples of similar bathymetric zonation have been reported in the bathyal turbinellid subfamily Columbariinae, along with the suggestion that such bathymetric speciation occurred as a result of sea level changes during the Cenozoic (Harasewych, 1986). In contrast to the zoogeographic patterns seen in the Columbariinae, where there is considerable divergence between Indian and Pacific ocean species, and close similarity between eastern and western Indian Ocean taxa (Harasewych, 1986), *Benthovoluta claydoni*, which occurs in comparable

depths, spans both oceans, ranging from off Western Australia to the Philippines.

Dendrograms showing UPGMA and single linkage clustering of the Recent genera included in Ptychatractinae, based shell and radular characters (table 8), are shown in figure 28. In each instance, the genera *Ceratoxancus* and *Latiromitra* are clustered together and differentiated from the other genera referred to Ptychatractinae. Although originally described in the family Turbinellidae, several authors have commented on the affinities of *Ceratoxancus* to the Mitridae (Sakurai, 1957) or Volutomitridae (Cernohorsky, 1973). The radulae and protoconchs of the two species in this genus are unknown. Prior to Bouchet and Waren's (1985) reassignment of *Latiromitra* to Ptychatractinae on the basis of overall conchological similarity to *Cyomesus*, this genus had been included in the families Buccinidae (Locard, 1897), Costellariidae (Thiele, 1929), and Volutomitridae (Cernohorsky, 1970). The radula of this monotypic genus is unknown. Bouchet and Waren (1985:255) commented on the multispiral protoconch of the type species, and suggested its larvae are planktotrophic. All members of the family Turbinellidae for which developmental data are available undergo direct development (Bandel, 1975a,b), and have large, bulbous, although occasionally multispiral, protoconchs (Vasinae—Abbott, 1959; Columbariinae—Darragh, 1969; Harasewych, 1983, 1986; Ptychatractinae—Bouchet & Waren, 1985; herein; Turbinellinae—Bandel, 1975b). Other than superficial conchological similarity, there is little evidence for inclusion of either of these genera in the family Turbinellidae. Determination of their true phylogenetic affinities will require anatomical and radular data.

The remaining genera have been referred to the Ptychatractinae on the basis of conchological as well as radular features. The close relationships between *Benthovoluta* and *Surculina* have been noted previously (Rehder, 1967; Kilburn, 1971). Although similar in shell morphology, these genera differ substantially in size (*Surculina* rarely exceeding 40 mm in length), bathymetric distribution (with a single exception *Surculina* inhabit depths in excess of 1,000 m), and geographic distribution (*Surculina* are known only from New Zealand and the eastern Pacific). Dall (1908) reported that the animal of *S. cortezi* (Dall, 1908) lacked eyes, tentacles and operculum. Although the loss of eyes is not uncommon in deep water gastropods (Knudsen, 1973; Harasewych, 1987), the absence of tentacles and opercula in these animals is enigmatic.

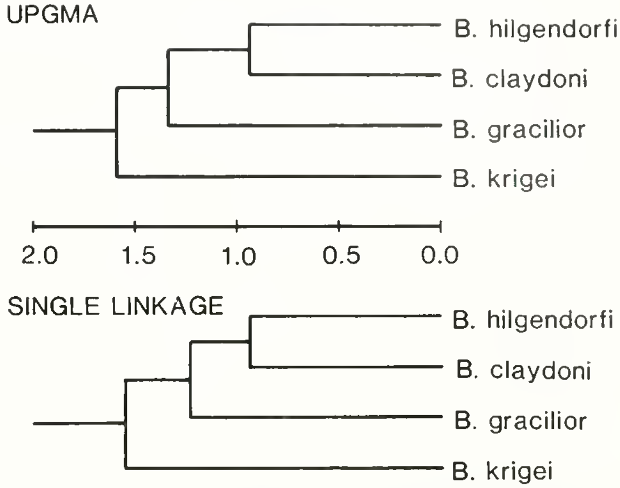


Figure 27. Phenetically deduced relationships between species in the genus *Benthovoluta*, produced by UPGMA (upper) and single linkage (lower) clustering of Euclidian distances between taxa, calculated using standardized data

Both clustering algorithms produced identical dendrograms of the relationships between the remaining small-shelled genera. *Cyomesus*, which is here regarded as distinct from *Latiromitra*, is the only Ptychatractine genus to have Recent representatives in the western Atlantic and western Pacific oceans. In his description of this genus, Quinn (1981:76) raised the possibility that the western Pacific representatives, which now include *Cyo-*

Table 7. Measurements of shell characters in the format mean/standard deviation. All linear measurements in mm. Mean values constitute the data matrix for phenetic analyses or relationships between *Benthovoluta* species.

Character	*hilgendorfi* n = 3	*claydoni* n = 5	*gracilior* n = 5	*krigei* n = 3
1) Sbc	2.75/0.01	2.88/0.10	2.63/0.17	3.24/0.11
2) Ssc	4.26/0.28	3.96/0.80	6.05/0.12	4.57/0.18
3) Rsl	0.68/0.06	0.68/0.04	0.99/0.11	0.70/0.10
4) beta	−1.6/1.4	−2.5/1.2	4.1/1.4	1.3/2.8
5) theta	12.2/2.2	11.5/1.4	11.9/0.6	11.4/0.3
6) W	1.38/0.02	1.49/0.03	1.47/0.01	1.58/0.05
7) D	0.18/0.04	0.22/0.04	0.17/0.00	0.15/0.05
8) T	7.64/0.36	7.50/0.47	8.43/0.55	9.14/0.67
9) A + SLC/SL	0.578/0.008	0.596/0.004	0.547/0.012	0.567/0.019
10) CP	0.0	0.0	0.0	1.0
11) C	1.0	0.0	0.0	1.0
12) Sut	0.0	0.0	0.0	1.0
13) Sculp	0.0	0.0	0.0	1.0

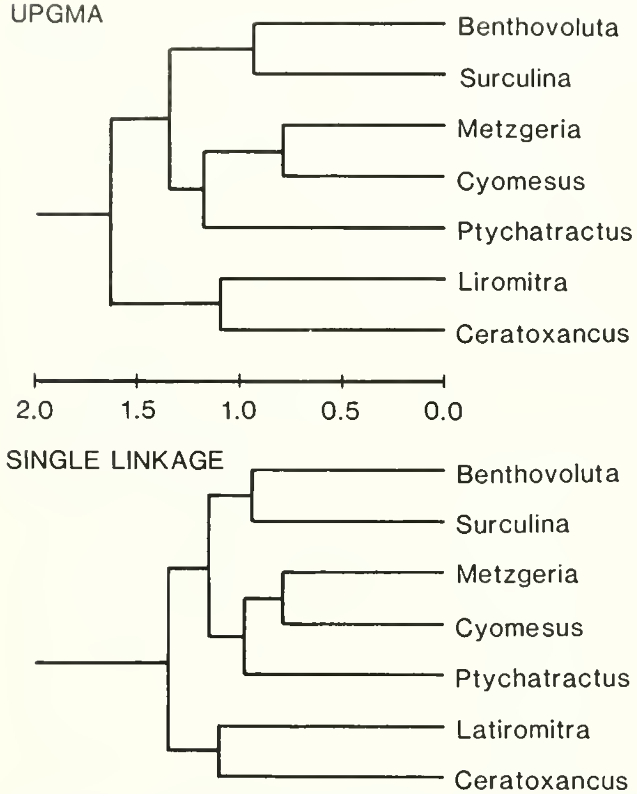


Figure 28. Phenetically deduced relationships between genera assigned to the subfamily *Ptychatractinae*, produced by UPGMA (upper) and single linkage (lower) clustering of Euclidian distances between taxa, calculated using standardized data.

mesus barthelowi (Bartsch, 1942), *C. delicatula* (Shikama, 1971), *C. sakashitai* (Habe, 1976), and *C. nakayasui* (Habe, 1976), might be separable into a separate subgenus. Most closely related to *Cyomesus*, or at least to its western Atlantic type species, is *Metzgeria*, from the bathyal zone of the northeastern Atlantic. These genera have very similar shell and radular morphologies as well as bathymetric ranges. Although several additional, geographically remote, species have been described in the genus *Metzgeria*, their generic assignments are considered either speculative (*M. californica* Dall, 1903; *M. montereyana* Smith and Gordon, 1948), being based on vague conchological similarities, or erroneous (*M. apodema* Bouchet and Talavera, 1981) by virtue of having a multispiral larval shell. More remotely related to both these taxa is *Ptychatractus*, the type genus of the subfamily. Similar to both genera in size and shell morphology, it is characterized by prominent spiral sculpture and by a radula that has features of *Cyomesus* as well as of *Benthovoluta* (figure 19).

Although fossil representatives of most of the Recent genera are unknown, a number of Cretaceous and Eocene genera have been regarded as possible members of the Ptychatractinae (Quinn, 1981). Examination of several specimens of the type species of *Paleofusimitra* Sohl, 1963 and *Fusimitra* Conrad, 1855 revealed only superficial similarity in shell form with any member of the Ptychatractinae. The similarity of the single known specimen of the Cretaceous genus *Mitridomus* Sohl, 1963 to *Latiromitra* had been noted by Sohl, 1964; however, resolution of the question of whether *Mitridomus* rep-

Table 9. Character state distributions of anatomical characters listed in table 5 among the subfamilies of Turbinellidae. COL = Columbariinae; PTY = Ptychatractinae; TUR = Turbinellinae; VAS = Vasinae.

Character	COL	PTY	TUR	VAS
1)	b	c	c	a
2)	a	a	b	a
3)	b	a	b	a
4)	b	b	b	a
5)	a	a	a	b
6)	a	a	a	b
7)	a	a	a	b
8)	a	a	b	a
9)	a	b	a	a
10)	a	b	b	a

Table 8. Measurements of shell characters used in phenetic assessment of the relationships of the Recent genera assigned to the subfamily Ptychatractinae. All linear measurements are in mm. BEN = *Benthovoluta*, CER = *Ceratoxancus*, CYO = *Cyomesus*, LAT = *Latiromitra*, MET = *Metzgeria*, PTY = *Ptychatractus*, SUR = *Surculina*.

Character	BEN	CER	CYO	LAT	MET	PTY	SUR
1) Sbc	2.75	2.67	2.23	2.17	2.00	1.63	2.44
2) Ssc	4.26	2.02	2.71	2.00	2.78	2.23	3.11
3) Rsl	0.68	0.41	0.72	0.41	0.60	0.50	0.73
4) beta	−1.6	−16.3	−4.1	−13.5	−4.8	−11.2	−0.5
5) theta	12.2	18.5	16.1	10.2	16.0	18.8	11.4
6) W	1.38	1.49	1.42	1.51	1.73	1.69	1.67
7) D	0.18	0.32	0.15	0.27	0.15	0.18	0.19
8) T	7.64	5.36	6.94	5.93	6.25	5.35	5.99
9) A + SLC/SL	0.58	0.55	0.59	0.47	0.54	0.51	0.60
10) Prot	1.0	?	1.0	0.0	1.0	1.0	1.0
11) Lat	1.0	?	0.0	?	0.0	1.0	1.0
12) Rach1	1.0	?	0.0	?	0.0	1.0	1.0
13) Rach2	1.0	?	0.0	?	0.0	0.0	1.0

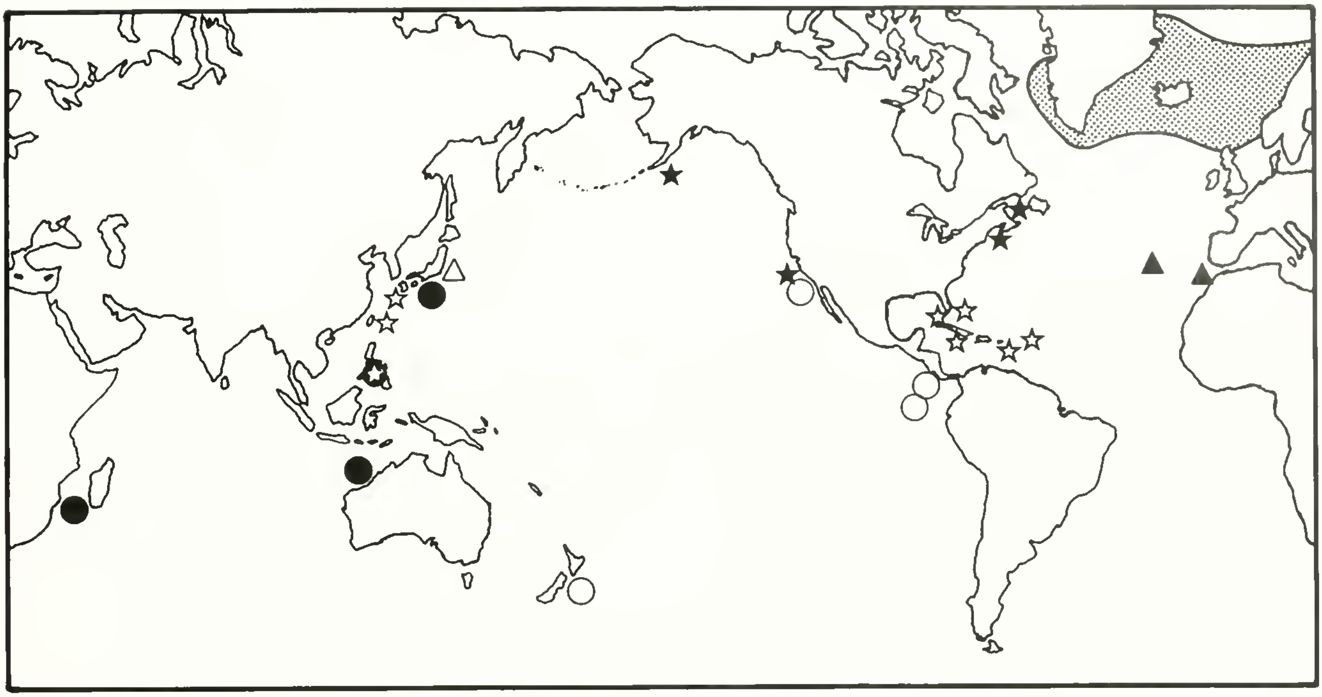


Figure 29. Recent geographic distribution of genera assigned to the subfamily Ptychatractinae. Open stars = *Cyomesus*; closed stars = *Ptychatractus*; open circles = *Surculina*; closed circles = *Benthovoluta*; open triangle = *Ceratoxancus*; closed triangles = *Latiromitra*; stippled area = *Metzgeria*.

resents an early ptychatractine, and *Latiromitra* a Recent descendant that retained a multispiral protoconch, or whether both genera had previously been correctly assigned to the family Mitridae, must await the availability of anatomical material of *Latiromitra*. Several species of the genus *Mesorhytis* Meek, 1876 from the Upper Cretaceous of the United States bear strong resemblance to Recent *Benthovoluta*, although they are smaller in size (about 30 mm). *Mesorhytis dakotaensis* Stanton, 1920 from Paleocene deposits of North Dakota, more closely resembles *Cyomesus*, and had a paucispiral protoconch. "*Fasciolaria*" *assimilis* Stoliczka, 1868 from the Upper Cretaceous of southern India, bears unmistakable resemblance to Recent species of *Benthovoluta*, and had attained a size of 140 mm. As inclusion of even Recent species in the Ptychatractinae on purely conchological characters is uncertain, the assignment of Cretaceous genera to this group must remain tentative.

The geographic distribution of the Recent genera of Ptychatractinae (figure 29) indicates that, with the single exception of *Latiromitra*, a monotypic genus with planktonic larvae questionably included in Ptychatractinae, all are restricted to continental margins or their adjacent abyssal plains. The distribution of the genus *Surculina* indicates that this group evolved in the Austral Province (Kauffman, 1973), prior to the separation of New Zealand at the end of the Early Paleocene, and is an offshoot of east Tethyan *Benthovoluta* or its precursors. The closing of the Tethys Sea at the end of the Eocene separated the Atlantic and Pacific species of the genus *Cyomesus*. The close resemblance of *Metzgeria* to the western Atlantic type species of *Cyomesus* suggests that *Metzgeria* is an offshoot from the west Tethyan branch of that genus. The origin of the genus *Ptychatractus* is more obscure. One possibility is that it diverged from the east Tethyan (western Pacific) branch of *Cyomesus*, evolved in the northern Pacific, with one branch extending southward along the western coast of North America, while another was part of the late Pliocene Beringean Transgression of Pacific boreal mollusks through the Bering Strait, across the Arctic, and into the North Atlantic (Durham & MacNeil, 1967; Nelson, 1978). The relationship of *Latiromitra* to the Cretaceous *Mitridomus* has been discussed previously. The affinities of *Ceratoxancus* are uncertain. If it is indeed a ptychatractine, it may be an offshoot of any of the equally questionable, mitriform, Cretaceous turbinellids.

Dissections of *Benthovoluta claydoni* new species revealed a basically turbinellid anatomical organization that most closely resembled *Turbinella angulata* in most features of the shell, mantle cavity, and alimentary and male reproductive systems, and *Coluzea rotunda* in features of the female reproductive system. The short muscular proboscis and torted, papillate penis, also found in *Cyomesus chaunax*, distinguish these taxa from all other turbinellids, and may prove to be diagnostic of the subfamily Ptychatractinae. The presence of an amphipod carapace in one stomach, as well as an absence of polychaete setae from the guts of all three of the specimens examined, suggest a diet different from that reported for the other subfamilies within Turbinellidae.

The phylogenetic relationships of the four subfamilies

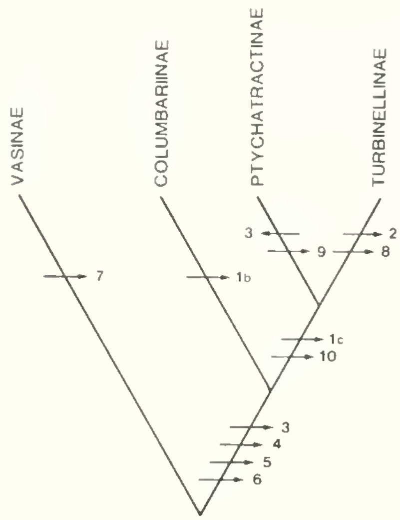


Figure 30. Cladograms indicating the relationships between the subfamilies of the family Turbinellidae, based on characters in table 5.

of Turbinellidae, as deduced from an analysis of the taxa in table 4 scored for the characters in table 5, are shown by the cladogram in figure 30. This cladogram, with a consistency index of 0.917, indicates that the subfamily Ptychatractinae is most closely related to the Turbinellinae, and that divergence between the Vasinae and the remaining subfamilies is the most ancient. This phylogenetic arrangement is at least partially supported by the fossil record, as the subfamilies Vasinae, Columbariinae, and Ptychatractinae all have Cretaceous representatives (Wenz, 1943; Darragh, 1969; herein), while earliest records of Turbinellinae date from the Lower Eocene (Vokes, 1964).

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LITERATURE CITED

Abbott, R. T. 1959. The family Vasidae in the Indo-Pacific. Indo-Pacific Mollusca 1(1):15–32.

Bandel, K. 1975a. Embryonalgehäuse karibischer Meso- und Neogastropoden (Mollusca). Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse Jahrgang 1975, Akademie der Wissenschaften und der Littratur, Mainz 1:4–133.

Bandel, K. 1975b. Entwicklung der Schale im Lebensablauf zweier Gastropodenarten; *Buccinum undatum* und *Xancus angulatus* (Prosobranchier, Neogastropoda). Biomineralisation 8:67–91.

Bandel, K. 1984. The radulae of Caribbean and other Mesogastropoda and Neogastropoda. Zoologische Verhandelingen 214:1–188, 22 pls.

Bartsch, P. 1942. Some deep-sea Philippine volutids. The Nautilus 56(1):9–13.

Bayer, F. M. 1971. New and unusual mollusks collected by R/V JOHN ELLIOTT PILSBURY and R/V GERDA in the tropical western Atlantic. Bulletin of Marine Science 21(1):111–236.

Bouchet, P. and F. G. Talavera. 1981. A new *Metzgeria* from northwest Africa. Bollettino Malacologico 17:177–180.

Bouchet, P. and A. Waren. 1985. Revision of the Northeast Atlantic bathyal and abyssal Neogastropoda excluding Turridae (Mollusca, Gastropoda). Bollettino Malacologico, Supplement 1, 296 p.

Cernohorsky, W. O. 1970. Systematics of the families Mitridae and Volutomitridae. Bulletin of the Auckland Institute and Museum 8:1–190.

Cernohorsky, W. O. 1972. A taxonomic evaluation of Recent and fossil non-mitrid species proposed in the family Mitridae (Mollusca: Gastropoda). Records of the Auckland Institute and Museum 9:205–229.

Cernohorsky, W. O. 1973. The taxonomy of *Benthovoluta hilgendorfi* (von Martens) and allied turbinellid genera (Mollusca: Volutacea). Records of the Auckland Institute and Museum 10:123–131.

Chapman, R. E., M. G. Harasewych, and R. Hershler. 1987. CONCH: an interactive computer program for the analysis of shell coiling parameters. Smithsonian Institution, Washington, DC. Prerelease version.

Clench, W. J. 1959. The genus *Columbarium* in the western Atlantic. Johnsonia 3(39):330–331.

Conrad, T. A. 1855. Observations on the Eocene deposits of Jackson, Mississippi, with descriptions of thirty-four new species of shells and corals. Proceedings of the Academy of Natural Sciences of Philadelphia 7:257–263.

Dall, W. H. 1903. A new species of *Metzgeria*. The Nautilus 17(5):51–52.

Dall, W. H. 1908. Reports on the dredging operations off the west coast of Central America . . . by the U.S. Fish Commission steamer "Albatross" . . . . Bulletin of the Museum of Comparative Zoology 43(6):205–487, 22 pls.

Dall, W. H. 1918. Changes in and additions to molluscan nomenclature. Proceedings of the Biological Society of Washington 31:137–138.

Darragh, T. A. 1969. A revision of the family Columbariidae (Mollusca: Gastropoda). Proceedings of the Royal Society of Victoria 83(1):63–119.

Durham, J. W. and F. S. MacNeil. 1967. Cenozoic migrations of marine invertebrates through the Bering Strait region. *In:* Hopkins, D. M. (ed.). The Bering Land Bridge. Stanford University Press, Stanford, CA. p. 326–349.

Fretter, V. and A. Graham. 1962. British prosobranch molluscs. Ray Society, London, 755 p.

Habe, T. 1952. Pholadomyidae, Clavagellidae, Pandoridae, Juliidae and Condylocardiidae in Japan. Illustrated Catalogue of Japanese Shells 18:121–132.

Habe, T. 1976. Two new species of the genus *Benthovoluta* Kuroda et Habe from the western Pacific. Venus 35(3): 97–100.

Harasewych, M. G. 1982. Mathematical modeling of the shells of higher prosobranchs. The Bulletin of the American Malacological Union, Inc. 1981:6–10.

Harasewych, M. G. 1983. A review of the Columbariinae (Gastropoda: Turbinellidae) of the western Atlantic with notes on the anatomy and systematic relationships of the subfamily. Nemouria 27:1–42.

Harasewych, M. G. 1986. The Columbariinae (Gastropoda: Turbinellidae) of the eastern Indian Ocean. Journal of the Malacological Society of Australia 7(3–4):155–170.

Harasewych, M. G. 1987. *Tractolira germonae*, a new abyssal Antarctic volute. The Nautilus 101(1):3–8.

Hatai, K. and S. Nishiyama. 1952. Checklist of Japanese Tertiary Marine Mollusca. The Science Reports of the Tohoku University, Sendai, Japan. Second Series (Geology) Special Volume 3, 464 p.

Hornell, J. 1914. The sacred chank of India, a monograph of the Indian conch (*Turbinella pyrum*). Madras Fisheries Bulletin 7:1–181.

Kauffman, E. G. 1973. Cretaceous Bivalvia. *In:* Hallam, A. (ed.). Atlas of palaeobiogeography. Elsevier, Amsterdam, p. 353–383.

Kensley, B. 1973. Sea-shells of South Africa. Gastropods. Maskew Miller, Ltd., Cape Town, 236 p.

Kilburn, R. N. 1971. Notes on some deep-water Volutidae, Turbinellidae and Turridae chiefly from off Southern Mocambique and Natal, with descriptions of two new species (Mollusca: Gastropoda). Annals Natal Museum 21(1):123–133.

Kira, T. 1962. Shells of the western Pacific in color. Hoikusha Publishing Co., Ltd., Osaka, 224 p.

Knudsen, J. 1973. *Guivillea alabastrina* (Watson, 1882), an abyssal volutid (Gastropoda: Mollusca). Galathea Report 12:127–131, pl. 18.

Kuroda, T. 1931. Two new species of Volutacea. Venus 3(1): 45–49.

Kuroda, T. 1952. On an interesting new genus of gastropod Mollusca from the sea off Kii Peninsula. Publications of the Seto Marine Laboratory 2(2):29–31.

Kuroda, T. 1965. On the generic position of *Benthovoluta* (Gastropoda). Venus 24(1):50–52.

Kuroda, T. and T. Habe. 1950. Volutidae in Japan. Illustrated Catalogue of Japanese Shells 1(5):31–38, pls. 5–7.

Kuroda, T., T. Habe, and K. Oyama. 1971. The sea shells of Sagami Bay. Maruzen Co., Ltd., 489 p., 121 pls., 51 p. index.

Lamarck, J. B. P. A. 1799. Prodrome d'une nouvelle classification des coquilles. Memoires de la Societe d'Histoire Naturelle de Paris 1:63–91.

Locard, A. 1897. Mollusques Testacés, I. Expeditions scientifiques du Travailleur et du Talisman. Masson, Paris, 516 p.

MacNeil, F. S. 1960. Tertiary and Quaternary Gastropoda of Okinawa. Geological Survey Professional Paper 339, 148 p., 19 pls.

von Martens, E. 1897. Conchologische Miscellen II. Archiv fur Naturgeschichte 63(1):157–180, pls. 15–17.

Meek, F. B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri Country. U.S. Geological Survey of the Territories Report 9:lxiv + 629 p.

Moses, S. T. 1923. The anatomy of the chank (*Turbinella pyrum*). Madras Fisheries Bulletin 17:105–127.

Nelson, C. M. 1978. *Neptunea* (Gastropoda: Buccinacea) in the Neogene of the North Pacific and adjacent Bering Sea. The Veliger 21(2):203–215.

Norman, A. M. 1879. The Mollusca of the fjords near Bergen. Journal of Conchology 2:8–77.

Ponder, W. F. 1973. The origin and evolution of the Neogastropoda. Malacologia 12(2):295–338.

Quinn, J. F. 1981. A new genus of Turbinellidae (Gastropoda: Prosobranchia), with the description of a new species from the Caribbean Sea. The Nautilus 95(2):72–77.

Rehder, H. A. 1967. A new genus and two new species in the families Volutidae and Turbinellidae (Mollusca: Gastropoda) from the western Pacific. Pacific Science 21(2): 182–187.

Sakurai, K. 1957. On a new species of Xancidae, *Cerato-xancus elongatus* (Gastropoda). Venus 19:161–163.

Shikama, T. 1963. Selected shells of the world illustrated in colours. Hokuryu-Kan Publishing Co., Ltd., Tokyo, 154 p., 102 pls.

Shikama, T. 1971. On some noteworthy marine Gastropoda from southwestern Japan (3). Science Reports Yokahama National University (2)18:27–35, pl. 3.

Smith, A. G. and M. Gordon, Jr. 1948. The marine mollusks and brachiopods of Monterey Bay, California and vicinity. Proceedings of the California Academy of Sciences, fourth series 26(8):147–245.

Sohl, N. F. 1963. New gastropod genera from the late Upper Cretaceous of the east Gulf Coastal Plain. Journal of Paleontology 37(4):747–757, pls. 89, 90.

Sohl, N. F. 1964. Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and Prairie Bluff formations. U.S. Geological Survey Professional Paper 331-B:153–344, pls. 19–52.

Stanton, T. W. 1920. The fauna of the Cannonball marine member of the Lance Formation. U.S. Geological Survey Professional Paper 128-A, 49 p., 9 pls.

Stimpson, W. 1865. On certain genera and families of zoophagous gastropods. American Journal of Conchology 1: 55–64.

Stoliczka, F. 1868. Cretaceous fauna of southern India. Gastropoda of the Cretaceous rocks of southern India. Memoirs of the Geological Survey of India, Paleontologia Indica, Vol. 2, Ser. 5, pts. 1–10, 497 p., 28 pls.

Swofford, D. L. 1985. PAUP, phylogenetic analysis using parsimony. Illinois Natural History Survey, Champaign, IL.

Taki, I. and K. Oyama. 1954. Matajiro Yokoyama's, The Pliocene and later faunas from the Kwanto region in Japan. Paleontological Society of Japan, Special Paper 2, 68 p., 49 pls.

Taylor, J. D., N. J. Morris, and C. N. Taylor. 1980. Food specialization and the evolution of predatory prosobranch gastropods. Paleontology 23(2):375–409.

Thiele, J. 1929. Handbuch der systematischen Weichtierkunde, I. G. Fischer, Jena, 376 p.

Vokes, E. H. 1964. The genus *Turbinella* (Mollusca, Gastropoda) in the New World. Tulane Studies in Geology 2(2): 39–68.

Wenz, W. 1938–43. Teil 6. Prosobranchia. *In:* Schindewolf, O. H. (ed.). Handbuch der Palaozoologie. Borntraeger, Berlin, vi + 1639 p.

Wilkinson, L. 1986. SYSTAT: the system for statistics. Systat, Inc., Evanston, IL.

Yokoyama, M. 1920. Fossils from the Miura Peninsula and its immediate north. Tokyo Imperial University, College of Science Journal 39(6):1–193, pls. 1–19.

The Freshwater Mussels (Unionidae) of the Upper Ohio River, Greenup and Belleville Pools, West Virginia

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ABSTRACT

A preliminary survey of freshwater mussels inhabiting areas around the Ohio River islands of West Virginia was conducted in 1983 by the U.S. Fish and Wildlife Service, assisted by the West Virginia Department of Natural Resources. This survey concluded that the Greenup and Belleville pools displayed a far greater abundance and diversity of mussels than the remaining navigational pools along West Virginia, and warranted further investigation. During the spring and summer months of 1985, numerous collections were made at various points within the two navigational pools to expand the data previously collected. Twenty-four species of unionid mussels and *Corbicula* were collected from these areas, representing 16 and 23 species from the Greenup and Belleville pools, respectively. No species on the federal endangered species list were encountered, however four of the species collected are considered endangered by the State of Ohio.

INTRODUCTION

A very limited amount of freshwater mussel research has been performed on the mainstem Ohio River within West Virginia The only recent studies were those conducted by Taylor (1980) and the U.S. Fish and Wildlife Service (1983) for the U.S. Army Corps of Engineers, Huntington District. Several of the major tributaries of the Ohio River have been surveyed by the West Virginia Department of Natural Resources, Division of Water Resources, in conjunction with a statewide inventory of mussel populations. These surveys include those by Zeto (1982) on the Monongahela River Basin, Schmidt *et al.* (1983) on the Little Kanawha River Basin, and Schmidt and Zeto (1983) on the Kanawha River. Other recent studies on these major Ohio River tributaries are those by Taylor (1983), Clarke (1982), and Morris and Taylor (1978), all on the Kanawha River. A review of literature records of the Muskingum River, Ohio has recently been prepared by Stansbery *et al.* (1985) for the U.S. Army Corps of Engineers, Huntington District.

It became evident from Taylor's 1980 Ohio River survey that a viable mussel population did exist in the river. This work, however, was based mainly on the collection of shell material and did not actually locate live mussel beds. The work performed by the U.S. Fish and Wildlife Service in 1983 indicated the presence of several extensive mussel beds closely associated with the Ohio River islands. The present survey represents a joint effort by the U.S. Fish and Wildlife Service and the West Virginia Department of Natural Resources, Division of Water Resources. The information presented was collected in 1983 and 1985 from locations in the Greenup and Belleville pools of the Ohio River. These data indicate that several of the mussel species presumed extirpated from the river are still present in isolated areas.

STUDY AREA

The Ohio River adjacent to West Virginia extends from the Ohio–West Virginia–Pennsylvania state line (RM 40.1) to the common corner of Ohio–Kentucky–West Virginia (RM 317.1), forming the state's western boundary with Ohio. The 277 miles of the river along West Virginia are composed of eight navigational pools, including the Greenup and Belleville pools (figure 1).

The Greenup pool is formed at Greenup lock and dam at RM 341.0 near Greenup, Kentucky, and extends upriver into West Virginia. The pool is 61.8 miles long and terminates at RM 279.2 at the Gallipolis lock and dam. Numerous locations were surveyed in the Greenup pool for freshwater mussels during the survey, including the two sites reported here that were found to support significant populations of mussels. Site 1 is located at RM 292.4 along the right descending bank near Green Bottom, Cabell County, West Virginia (38°34′25″N, 82°17′34″W). The substrate consists of sand, gravel, cobble, and boulders. Site 2 is located at the head of Lesage Island (RM 289) near the common boundary of Mason and Cabell counties, West Virginia and Gallia County, Ohio (38°14′17″N, 82°14′54″W). Substrate at this location consists primarily of sand, gravel, and cobble.

The Belleville pool originates at Belleville lock and dam at RM 203.9 at Belleville, Wood County, West Vir-

ginia. The pool terminates upriver at the Willow Island lock and dam, and has a total length of 42.1 miles. Five sites were chosen from those surveyed for inclusion in this report. Site 3 is located farthest down-river of the Belleville pool sites. It is situated at the head and back channel of Neal Island near Parkersburg, Wood County, West Virginia at RM 181.1 to RM 182 (39°18′37″N, 81°33′24″W). Substrate varies from sand, gravel, and cobble at the island head to a combination of silt, sand, and gravel in the back channel. Site 4 is situated below the toe of Vienna (Halfway) Island near Vienna, Wood County, West Virginia (39°20′22″N, 81°33′26″W). The mussel bed extends from RM 179 to RM 179.9, and has a substrate consisting of sand, gravel, and cobble. Site 5 is located at the head of Vienna (Halfway) Island, extending into the back channel of the island. This site is also located near Vienna, Wood County, West Virginia at RM 178.1 (39°21′24″N, 81°32′28″W). The substrate is mainly composed of silt, sand, and gravel. Site 6 extends from above the head of Muskingum Island (RM 175.2) through its back channel and onto the toe of the island (RM 177.4), where the bed is situated near the navigation channel. Muskingum Island lies approximately 3 miles northeast of Vienna, Wood County, West Virginia (39°22′00″N, 81°32′19″W). This island back channel has substrate consisting primarily of silt, sand, and gravel. Site 7 lies entirely in the back channel of Marietta (Buckley) Island at RM 169.1 near Williamstown, Wood County, West Virginia (39°23′14″N, 81°24′43″W). The substrate at this site is composed of silt, sand, and gravel. Sampling sites are depicted in figure 1.

Figure 1. Ohio River, West Virginia. Sampling sites are indicated. Specific locations are identified in text.

METHODS

Sampling sites were chosen by one of two methods. The first method involved "follow-up" surveys of areas surrounding the Ohio River islands. The initial study of these island areas was conducted by the U.S. Fish and Wildlife Service (1983), and indicated that several of these island areas in the Greenup and Belleville pools had a very rich mussel fauna. The second method of site selection was simply choosing areas in the river associated

Table 1. Freshwater mussels of the Ohio River, Greenup pool, West Virginia

Species	Site number 1	Site number 2	Total number collected	Percent relative abundance
Strophitus undulatus undulatus (Say, 1817)		1[1]	1	0.26
Lasmigona complanata (Barnes, 1823)		2	2	0.53
Quadrula quadrula (Rafinesque, 1820)	14	87	101	26.65
Quadrula metanevra (Rafinesque, 1820)	10	28	38	10.03
Quadrula pustulosa pustulosa (Lea, 1831)	13	20	33	8.71
Amblema plicata plicata (Say, 1817)	3	10	13	3.43
Fusconaia flava (Rafinesque, 1820)		1	1	0.26
Plethobasus cyphyus (Rafinesque, 1820)		7	7	1.85
Pleurobema cordatum (Rafinesque, 1820)	14	2	16	4.22
Elliptio crassidens crassidens (Lamarck, 1819)	103	8	111	29.29
Obliquaria reflexa (Rafinesque, 1820)	1	8	9	2.37
Actinonaias ligamentina carinata (Barnes, 1823)	9		9	2.37
Leptodea fragilis (Rafinesque, 1820)		2	2	0.53
Potamilus alatus (Say, 1817)	1	2	3	0.79
Ligumia recta (Lamarck, 1819)	2	1	3	0.79
Lampsilis ventricosa (Barnes, 1823)	26	4	30	7.92
Total	11	15	379	100.00

NOTE: *Corbicula* sp. was also found at each sampling location.
[1] Fresh dead shell

Table 2. Freshwater mussels of the Ohio River, Belleville pool, West Virginia.

Species	Site number					Total number collected	Percent relative abundance
	3	4	5	6	7		
Anodonta imbecillis (Say, 1829)	1	1		1		3	0.27
Anodonta grandis grandis (Say, 1829)				1[1]	1[1]	2	0.18
Strophitus undulatus undulatus (Say, 1817)		1		1		2	0.18
Lasmigona complanata (Barnes, 1823)	4	1	1	3		9	0.82
Magnonaias nervosa (Rafinesque, 1820)			4			4	0.36
Quadrula quadrula (Rafinesque, 1820)	67	339	89	273		768	69.63
Quadrula metanevra (Rafinesque, 1820)	1	12		6		19	1.72
Quadrula pustulosa pustulosa (Lea, 1831)	1	14	2	24	6	47	4.26
Amblema plicata plicata (Say, 1817)	8	82	10	49	11	160	14.51
Fusconaia flava (Rafinesque, 1820)	5[1]			5[1]		10	0.91
Plethobasus cyphyus (Rafinesque, 1820)		1				1	0.09
Pleurobema cordatum (Rafinesque, 1820)		3		1		4	0.36
Elliptio crassidens crassidens (Lamarck, 1819)		1				1	0.09
Uniomerus tetralasmus (Say, 1831)			1			1	0.09
Obliquaria reflexa (Rafinesque, 1820)	2	15		4		21	1.90
Actinonaias ligamentina carinata (Barnes, 1823)				1		1	0.09
Obovaria subrotunda (Rafinesque, 1820)		2		3		5	0.45
Truncilla donaciformis (Lea, 1827)	3	7	3	2		15	1.36
Leptodea fragilis (Rafinesque, 1820)	3	1	1	1	1	7	0.64
Potamilus alatus (Say, 1817)	3	5	3[1]	4		15	1.36
Potamilus ohiensis (Rafinesque, 1820)	1			1[1]		2	0.18
Lampsilis radiata luteola (Lamarck, 1819)		1[1]				1	0.09
Lampsilis ventricosa (Barnes, 1823)	1	1		3		5	0.45
Total	13	17	9	18	4	1103	99.99

NOTE: *Corbicula* sp. was also found at each sampling location.
[1] Fresh dead shell.

with the force of the thalweg, mainly river bends. River bends are generally "clean-swept" by the river's current and are likely areas for mussels to populate, especially near the outside of the turn.

The primary method of sampling was by brailing, utilizing both dovetail and crowfoot brail hooks. Shallow water and the shoreline were also surveyed for fresh-dead shells and midden piles. However, at the sites surveyed the vast majority of the mussel beds were located in 12–18 feet of water. As material was collected in the field, a preliminary species list was compiled on site. A suitable number of individuals were retained for positive identification and as voucher specimens. These have been accessioned in the Ohio State University Museum of Zoology. Dr. David Stansbery aided in the identification of the specimens.

RESULTS

A total of 24 species of freshwater unionid mussels as well as the Asiatic clam *Corbicula* were collected from the areas surveyed. The Greenup pool (table 1) supported 16 species of mussels, with the dominant species *Elliptio crassidens crassidens* and *Quadrula quadrula* having respective relative abundances of 29.29 and 26.65% of the population sampled. A significant portion of the mussel fauna in this pool was also comprised of *Quadrula metanevra* and *Quadrula pustulosa pustulosa*, representing 10.03 and 8.71% of the sample, respectively. The population of Site 1 was dominated by *E. c. crassidens*, while *Q. quadrula* was dominant at Site 2. The occurrence of *E. c. crassidens* at Site 1 represented the most significant population of this species, once thought to be extirpated from the upper Ohio River, in this portion of the river.

The Belleville pool was apparently more diverse in species composition than the Greenup pool, supporting 23 species of unionid mussels, in addition to *Corbicula* (table 2). By far the dominant species in the Belleville pool was *Q. quadrula*, which had a relative abundance of nearly 70%, followed by *Amblema plicata plicata*, comprising 14.51% of the population. This situation also held true for individual site analyses of areas 3, 4, 5, and 6. At Site 7, however, a drastic decrease of species diversity and total population was apparent, as only four species were collected at this site. Investigation of numerous sites in the remaining 7 miles (RM 162–169) of the Belleville pool above Site 7 indicated that this region of the Ohio River was nearly devoid of unionids. Only a few (< 10) specimens of *Q. quadrula* and *A. p. plicata* were taken in this upper 7 mile reach of the Belleville pool.

DISCUSSION

The authors believe the greater species diversity in the Belleville pool is influenced by several factors. Several

major rivers (Muskingum and Little Kanawha) enter the Ohio River in the Belleville pool close to the study areas. These rivers contain significant mussel populations (Schmidt *et al.*, 1983; Stansbery *et al.*, 1985) which undoubtedly have contributed to the Ohio River fauna. The Belleville pool also contains numerous islands within its boundaries. The back channels of these islands not only provide a refuge from navigational and dredging impacts, but also provide a variety of habitats for mussel populations. In comparison, the tributaries of the Greenup pool are believed to have little influence on the Ohio River mussel populations, and there is also far less island habitat in this pool.

In comparing the relative abundances of the mussel populations in the two pools surveyed, it is very apparent that the Greenup pool has a more evenly dispersed faunal representation than the Belleville pool. This may be attributed to the smaller amount of industrialization and somewhat isolated condition existing in the study area of the Greenup pool, resulting in fewer negative impacts to the river.

Several species collected during this survey had been presumed extirpated from the Ohio River in West Virginia (Taylor, 1980). These species are: *Elliptio crassidens crassidens*, *Actinonaias ligamentina carinata*, *Plethobasis cyphyus*, *Ligumia recta*, *Truncilla donaciformis* (later reported present by Taylor, The Ohio River Biology Symposium, Huntington, WV, 1984). Four of the species collected, *Quadrula metanevra*, *Plethobasis cyphyus*, *Pleurobema cordatum*, and *Potamilus ohiensis*, are considered endangered by the State of Ohio (Stansbery, 1976). No species listed as endangered by the federal government were encountered.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Clarke, A. H. 1982. Survey of the freshwater mussels of the Upper Kanawha River (RM 91–95). Fayette County, West Virginia, with special reference to *Epioblasma torulosa torulosa* and *Lampsilis abrupta*. U.S. Fish and Wildlife Service, Newton Corner, MA, 104 p.

Morris, J. S. and R. W. Taylor. 1978. A survey of the freshwater mussels of the Kanawha River of West Virginia. The Nautilus 92(4):153–155.

Schmidt, J. E. and M. A. Zeto. 1983. A survey of the freshwater mussel fauna of the Kanawha River September 1981–September 1982. Proceedings of the West Virginia Academy of Sciences 55(2–4):72–75.

Schmidt, J. E., M. A. Zeto, and R. W. Taylor. 1983. A survey of the mussel fauna of the Little Kanawha River Basin. Report of Freshwater Mussels Workshop, 26–27 October 1982. U.S. Army Engineers Waterways Experiment Station, Vicksburg, MS, 196 p.

Stansbery, D. H. 1976. Ohio's endangered naiad mollusks. Annual Meeting of the American Malacological Union.

Stansbery, D. H., K. E. Newman, K. G. Borror, and C. B. Stein. 1985. Literature records of bivalve mollusks of the Muskingum River system, Ohio. U.S. Army Corps of Engineers, Huntington District, 472 p.

Taylor, R. W. 1980. A survey of the freshwater mussels of the Ohio River from Greenup locks and dam to Pittsburgh, Pennsylvania. U.S. Army Corps of Engineers, Huntington/Pittsburgh Districts, 71 p.

Taylor, R. W. 1983. A survey of the freshwater mussels of the Kanawha River. U.S. Army Corps of Engineers, Huntington District, 62 p.

U.S. Fish and Wildlife Service, Department of the Interior. W. A. Tolin and P. A. Schettig (principal investigators). 1983. A physical and biological survey of the Ohio River islands (Huntington District). 315 p.

Zeto, M. A. 1982. Notes on the freshwater mussels (Unionidae) of the Upper Monongahela River Basin, West Virginia. The Nautilus 96(4):127–129.

New Distributional Records for *Polygyriscus virginianus* (Burch, 1947) (Pulmonata: Helicodiscidae)

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INTRODUCTION

Because of its secretive habits, few specimens of the Virginia fringed mountain snail have ever been seen. Solem (1976) regarded this species as one of the rarest snails in North America and in 1978 it was placed on the Federal Endangered Species List (U.S. Government Document, 1978). Of the 146 documented specimens collected since 1937, only 27 were live collected. In 1948 Burch found two living adults (Hubricht, personal communication), Hubricht (1972) found 21 (14 adults, seven juveniles) in 1971 and Grimm (1981) found three adults. All of these were collected from a single talus rock pile (type locality) at the base of high limestone (Elbrook formation) bluffs along the New River in Pulaski County, Virginia. Except for a single shell found 6.6 km southwest of the type locality in 1937, all specimens collected prior to 1981 were found in or near this 9 square meter rock pile.

Grimm (1981) expanded the range of this snail to include four additional sites within 1 km of the type locality. All 26 living specimens collected through 1981, however, were confined to the type locality, and all specimens were found 25 cm or deeper in the substrate. This report documents the collection of the 27th living specimen, and includes a range extension represented by four additional shells (voucher specimens USNM 859139, USNM 859140, and USNM 859141).

To date, *Polygyriscus virginianus* has been found associated only with weathered Elbrook formation (Cambrian) dolomitic limestone along the New River bluffs in Pulaski County, Virginia. This secretive species has been described as a burrowing calciphile (Hubricht, 1985), and has been found burrowing at 10 cm to 60 cm depths in fragmented limestone mixed with rootlets and a clayey soil (Grimm, 1981; Batie, 1986). It is associated with permanently damp soil under limestone talus at the base of high bluffs. The talus slopes are usually heavily shaded, vine-covered, and with little accumulated humus or organic matter.

METHODS

An area within a 16.1 km (10 mile) radius around the known habitat was searched for over 300 hr during a year-long effort (July, 1985–August, 1986) to establish the actual distribution of this species. Soil samples from nearly 200 holes, each measuring 25 cm across and 45–60 cm deep, were collected with a garden trowel and sifted using a 2.0 mm screen in tandem with a 0.5 mm screen. Snails were hand picked from the screens and examined in the field with a 7–10 × hand lens.

RESULTS

During the study, 30 adult specimens were collected. Of these, 25 empty shells and one living snail were collected within about 1.1 km of the type locality. Four additional shells were collected at sites up to 3.3 km northeast of the type locality. This range extension gives a total documented range of only 9.9 km for shells of this species. Although no living snails were found at the new northeast sites, a single living snail was observed and released 70 m southwest of the type locality at 10 cm depth. Living snails have now been documented only along a 70 m stretch of the river bluffs.

Although previous studies (Burch, 1947; Grimm, 1981; Hubricht, 1985) indicated that this species was found only at depths exceeding 25 cm, with most being found at the 45 cm level, Solem (1976) indicated that *Polygyriscus* may move to the surface during wet weather. Finding this single live specimen at the 10 cm level on moist rock fragments strengthens Solem's argument. It thus seems that *Polygyriscus* can exist in a somewhat broader vertical zone than was previously reported. No surface activity, however, was noted during nearly 14 hr of rainy, nighttime collecting.

LITERATURE CITED

Batie, R. E. 1986. Distribution and abundance of *Polygyriscus virginianus* (Burch, 1947), the Virginia fringed mountain snail. Contract Report to the Virginia Commission of Game and Inland Fisheries, Richmond, VA, 27 p.

Burch, P. R. 1947. *Polygyra virginiana*, a new species from Virginia. The Nautilus 61(2):40–41.

Grimm, F. W. 1981. Distribution, habitat requirements and recovery needs of the endangered land snail, *Polygyriscus*

virginianus. Contract Report to the U.S Fish and Wildlife Service. Washington, DC, 17 p.

Hubricht, L. 1972. Two new North American Pulmonata: *Paravitrea seradens* and *Philomycus sellatus*. The Nautilus 86(1):16–17.

Hubricht, L. 1985 The distribution of the native land mollusks of the eastern United States. Fieldiana: Zoology, new series 24:1–191.

Solem, A 1976. Endangered status of eastern United States land snails. Contract Report to the U.S. Fish and Wildlife Service, Washington, DC. OES Contract Number 14-16-0008-764, 9 p.

U.S Government Document 1978. Determination that seven eastern U.S. land snails are endangered or threatened species. Federal Register 43(128), July 3:28932–28935

Sympatric Occurrence of Living *Nautilus* (*N. pompilius* and *N. stenomphalus*) on the Great Barrier Reef, Australia

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ABSTRACT

Two species of *Nautilus*, *N. pompilius* Linnaeus, 1758 and *N. stenomphalus* Sowerby, 1849, inhabit the deep forereef slopes off Lizard Island, on the Great Barrier Reef. Of 29 specimens trapped at 250–440 m depth, 11 are typical of the widespread species *N. pompilius*, seven others show shell characteristics of *N. stenomphalus*, and exhibit a unique, strongly nodose hood texture; 11 specimens show features that are intermediate between these two species. The Lizard Island record represents the first known locale where living specimens of *N. stenomphalus* have been found, the second example of sympatric species of *Nautilus*, and it may be the first known example of hybridization between two species of *Nautilus*.

INTRODUCTION

The presence of living *Nautilus* on Australia's Great Barrier Reef has long been suspected on the basis of the fairly common presence of drifted shells. Iredale (1944) even erected a species for the North Queensland drift shells (*N. alumnus* Iredale, 1944). Another species (*N. stenomphalus* Sowerby, 1849) was thought to occur there as well. A third species, *N. repertus* Iredale, 1944, was named for drift shells thought to originate from southern and western Australian waters. Nevertheless, the only published accounts of Australian *Nautilus* consist of descriptions of isolated drift shells (Iredale, 1944; Cotton, 1957) and a few reports of beach-stranded or trawled specimens (*e.g.*, Riddle, 1920); no systematic description or analysis of any of this material has previously been undertaken.

The present account is a report on the successful results of deep-water trapping for *Nautilus*, during June and December, 1985, off Lizard Island, Queensland (figure 1). Twenty-nine specimens were obtained, that appear to include two distinct species: *Nautilus pompilius* Linnaeus, 1758 and *N. stenomphalus* Sowerby, 1849. The Great Barrier Reef occurrence of *Nautilus* is important in that it includes the first living specimens referable to *N. stenomphalus*, and it is only the second known occurrence of sympatric species of *Nautilus* (Saunders *et al.*, 1987).

Following is a brief description of the specimens; 18 conform to the definitions of either *N. pompilius* or as *N. stenomphalus*. The remainder exhibit characteristics that are to varying degrees intermediate between the two species, and they are accordingly identified as *N. pompilius*? or as *N. stenomphalus*? (figure 2). These intermediate forms appear to represent hybridization between sympatric species of *Nautilus*.

MATERIALS AND METHODS

Grouper- and mackrel-baited, baffle-style traps, measuring *ca.* 1 m × 1 m × 2 m were set at depths of 140 m to approximately 440 m, off Carter Reef, just north of Cook's Passage, approximately 20 km northeast of Lizard Island, Queensland (figure 1). Traps were buoyed at the surface, and, when possible, were retrieved after one to three nights. Overall, the trap yields were sparse compared to those obtained at other *Nautilus* trapping sites; the highest yield was five animals, in an overnight trap at 400–440 m depth. By comparison, as many as 34 and 67 *Nautilus* per trap were obtained in Papua New Guinea and in Palau, respectively (Saunders & Ward, 1987; Saunders *et al.*, 1987). On the Great Barrier Reef, however, high surface currents combined with steep bottom slopes caused extensive trap drifting, making any conclusions regarding depth distribution or relative abundance of *Nautilus* in this area tentative. Following retrieval, animals were measured, weighed, sexed, photographed, and tissue samples were taken for electrophoretic analysis. Reference specimens have been reposited with the Australian Museum, Sydney (AM C 148211, 148212, 148214–148216), the American Museum of Natural History, New York (Lz 24), and at the National Museum of Natural History, Washington, D.C. (USNM 816710–816713).

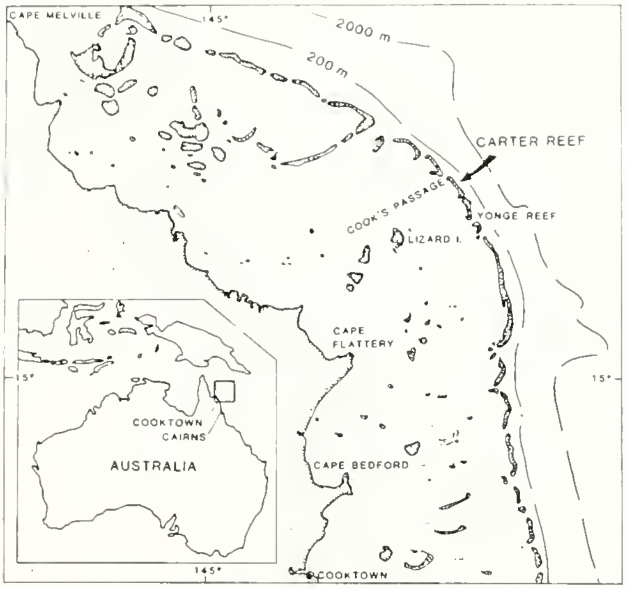


Figure 1. Location map showing deep-water trapsite off Carter Reef, Great Barrier Reef, Queensland, where *Nautilus pompilius* and *N. stenomphalus* were obtained at 250–440 m depth.

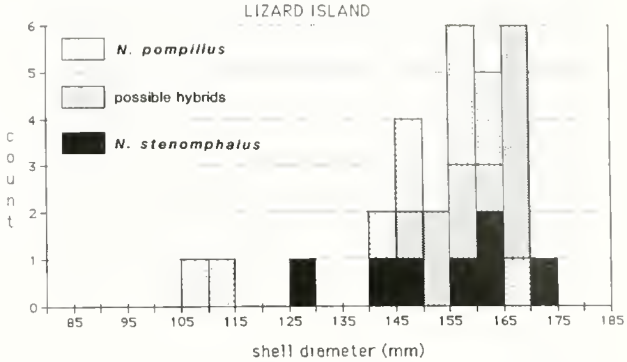


Figure 2. Frequency distribution showing maximum shell diameter of 29 live-caught specimens of *N. pompilius*, *N. stenomphalus*, and intermediates or presumed hybrids (*N. pompilius?*, *N. stenomphalus?*).

DESCRIPTION

Nautilus pompilius Linnaeus, 1758

Typically, the shell of *N. pompilius* is *ca.* 165 mm diameter and has a small umbilicus that is filled with a callus, with but rare exceptions (Saunders, 1981, 1987; Saunders *et al.*, 1987). Shell coloration is variable, but characteristically exhibits irregularly bifurcating, radial brown stripes extending from umbilicus to venter (figures 7, 12). The reddish-brown hood is covered with low, rounded, white elevations, giving it a mottled, slightly bumpy appearance (figures 7, 8).

The 11 specimens of *N. pompilius* available for study from the Great Barrier Reef differ in no major respect from conspecific specimens from the Philippines. They are slightly smaller, with a mean mature shell diameter of 155.2 mm, and mean weight (body plus shell) of 640.6 g (table 1). The pattern of shell coloration is also similar, with the exception of two specimens (Lz 5, 13) that lack color banding in the umbilical region. This same pattern characterizes *N. stenomphalus* but it also occurs as a rare variation in populations of both *N. pompilius* and *N. belauensis*. The color of the banding in most specimens is brick-red, which is typical of the species. One specimen (Lz 13) exhibits yellow-brown stripes; such coloration is thought to characterize the questionable Australian taxon *N. repertus* (Saunders, 1981, 1987). The color bands of the Lizard Island specimens do not coalesce across the ventral region. In this respect they more closely resemble typical *N. pompilius* from the Philippines than the geographically closer forms from Papua New Guinea (Saunders & Davis, 1985; Saunders *et al.*, 1987). Many of these generalizations, however, could require amendment as more specimens become available for study.

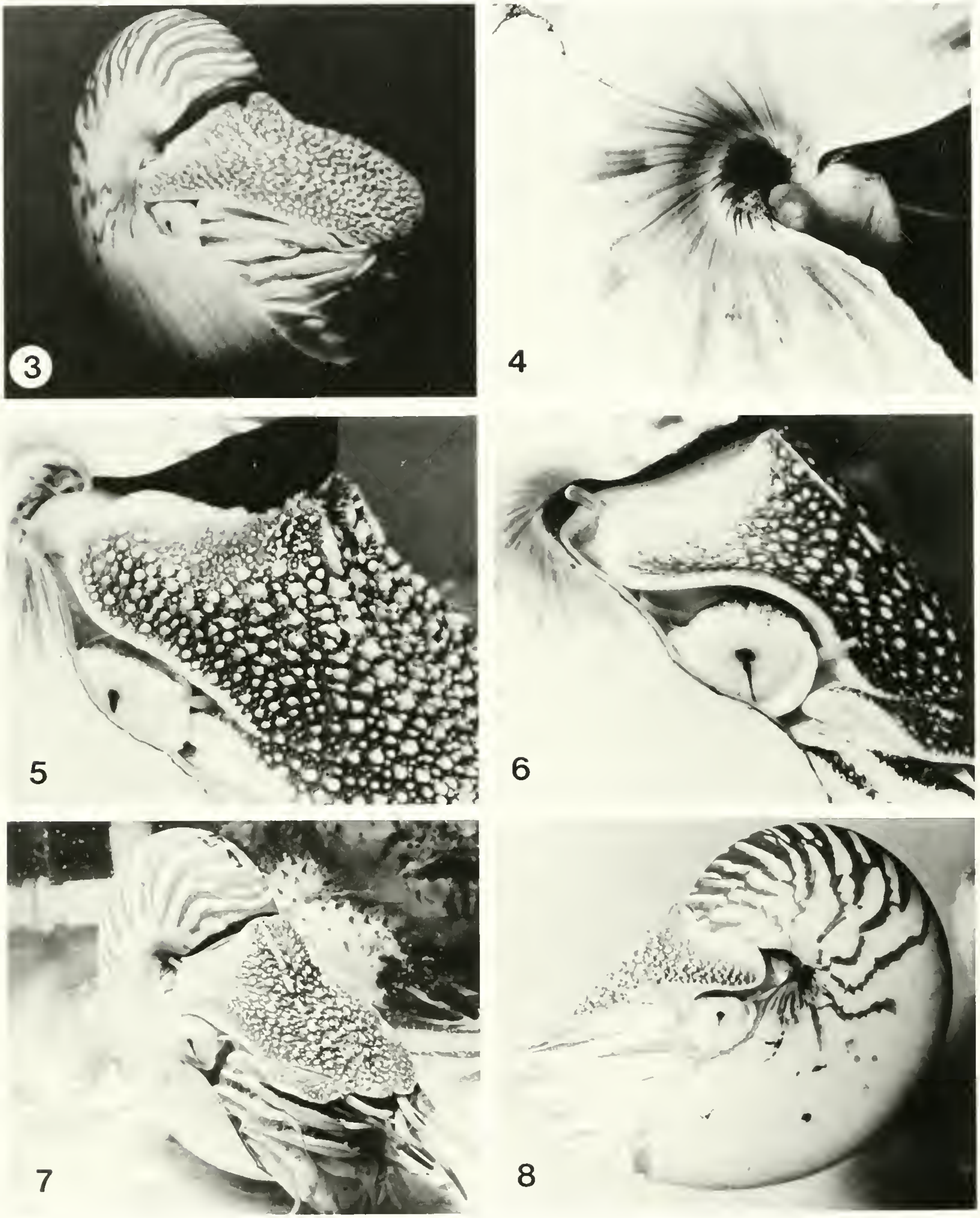
Nautilus stenomphalus Sowerby, 1849

The shell form is similar, if not identical, to *N. pompilius*, except that the umbilicus is open, lacking a callus, and shell coloration is reduced, lacking stripes in the umbilical region (figures 3–5, 9, 11). The surface of the hood exhibits a rough, nodose texture that is produced by a series of highly irregular papillae (figures 3, 5). This texture may extend to some of the tentacular sheaths as well.

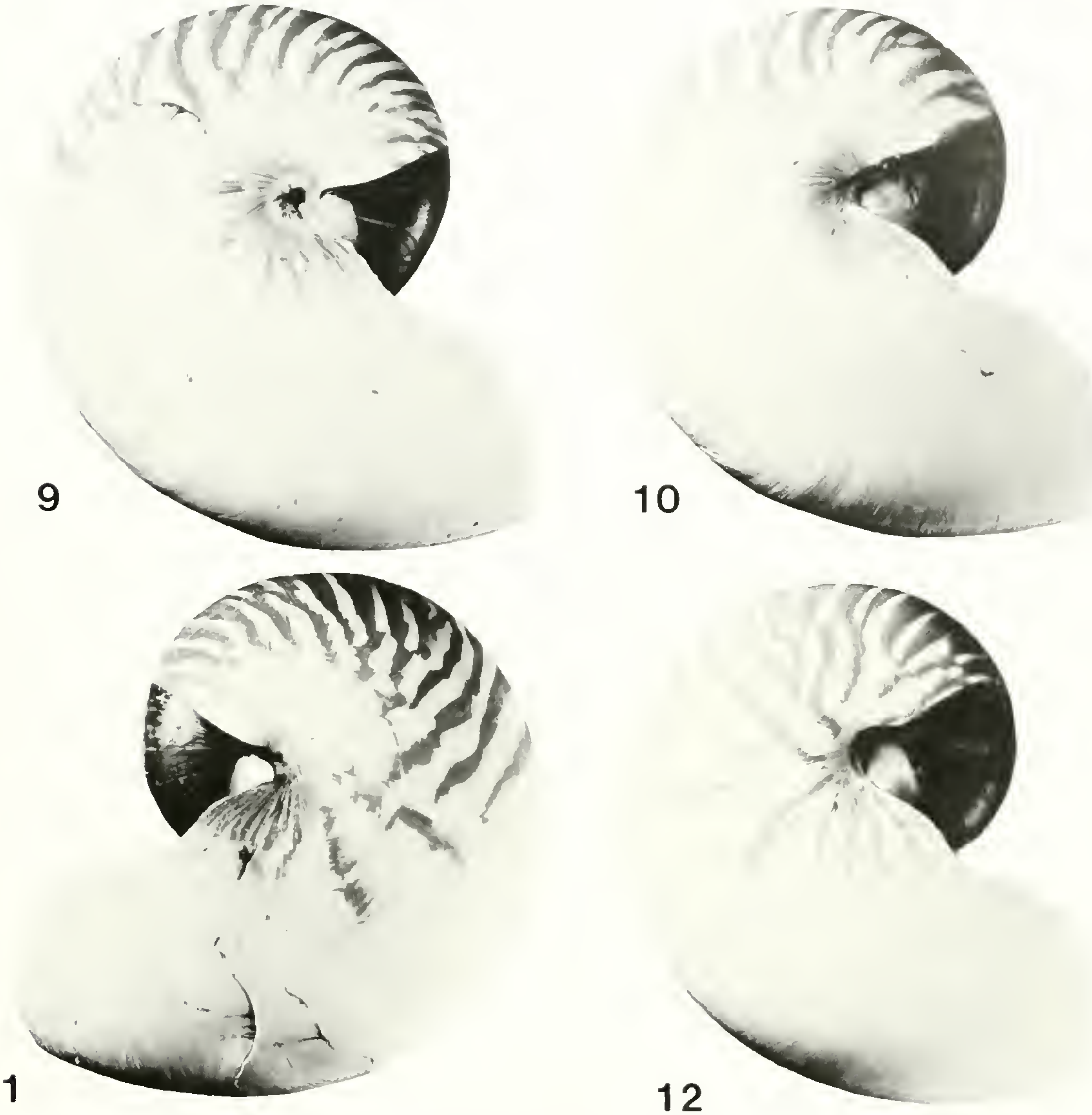
Seven of the 29 specimens of *Nautilus* obtained from the Great Barrier Reef are attributable to *N. stenomphalus*, heretofore known only from drifted shells. This species is similar in size to *N. pompilius* (figure 2) with

Table 1. Data from mature *N. stenomphalus* and *N. pompilius* from Carter Reef, off Lizard Island, Great Barrier Reef

	Sex	Shell diameter (mm)			Shell width (mm)			Total weight (g)		
		Range	Mean	SD	Range	Mean	SD	Range	Mean	SD
Nautilus stenomphalus	Females (n = 2)	141.7–147.8	144.8	4.3	63.3–64.3	63.8	0.5	422–480	451	41
	Males (n = 4)	157.9–170.4	163	5.3	74.2–80.3	76.6	2.7	650–730	682.5	39.5
	Total (n = 6)	141.7–170.4	156.9	10.5	63.3–80.3	72.3	6.9	422–730	605.3	124.8
Nautilus pompilius	Females (n = 2)	142.3–154.8	148.6	—	60.3–73	66.7	—	—	—	—
	Males (n = 8)	147.2–165.2	156.9	6.16	67.2–77.4	73.7	3.5	540–710	641.4	70.9
	Total (n = 10)	142.3–165.2	155.2	7.1	60.3–77.4	72.3	5.2	540–710	640.6	65.7



Figures 3–8. Photographs of living *Nautilus stenomphalus* (3, 4, 5, 8) and *N. pompilius* (6, 7) from Carter Reef, Queensland. **3.** *N. stenomphalus* (Lz 7) photographed in shallow water, showing characteristic open umbilicus, lack of umbilical coloration, and distinctively textured hood (× ½ approx.). **4, 5.** *N. stenomphalus*, closeup views of open umbilicus and distinctive, nodose hood texture (Lz 6, USNM 816711, × 2, × 1). **6, 7.** *N. pompilius* showing typical hood texture (6) and full view of animal in aquarium (Lz 1, × 1, × ½). **8.** *N. stenomphalus*?, an intermediate form, exhibiting nodose hood texture of *N. stenomphalus* with shell coloration of *N. pompilius* (× ½). Photograph (1) by T. Landry, (7, 8) by B. Goldman



Figures 9–12. Shells of live-caught *N. pompilius* and *N. stenomphalus* from Carter Reef, Queensland. **9, 11.** *N. stenomphalus* (Lz 6, USNM 816711; Lz 25, USNM 816712). **10.** *N. stenomphalus*?, with umbilical callus (Lz 3, USNM 816713). **12.** *N pompilius* (Lz 2, USNM 816710). All figures × ½.

a mean shell diameter of 156.9 mm, and a mean weight (body plus shell) of 605.3 g. The nodose hood texture appears to be unique among the species of *Nautilus*; in all of the dozen or so populations of *N. pompilius* examined to date, as well as in *N. macromphalus* and *N. belauensis*, the hood markings and texture are the same—reddish-brown, mottled with low, white bumps (figures 6, 7). Only *N. scrobiculatus* differs in this regard; its hood is covered with closely spaced, conical elevations (Saunders *et al.*, 1987: figs. 7, 8).

All seven of the specimens identified as *N. stenomphalus* (*i.e.*, those that have an open umbilicus and lack umbilical color bands) show the uniquely textured hood, it being more or less equally developed in each. The surface of some of the outer tentacular sheaths, which, like the hood, are composed of non-muscular, cartilaginous tissue, also show an irregular, somewhat digitated appearance that has not been previously noted among the other described species of *Nautilus*.

DISCUSSION

In considering the relationship between *N. pompilius* and *N. stenomphalus*, it is important to note that both species were originally described solely on the basis of shell characteristics. Sowerby (1849:465, pl. 98, fig. 3) distinguished the latter by its small, open umbilicus, and by the color pattern, in which the stripes do not extend to the umbilicus. The locality for Sowerby's figured specimen was not cited. Little else has been known of this

Table 2. Tabulation of sex, maturity, and species-distinguishing characteristics in *Nautilus pompilius* and *N. stenomphalus* from Carter Reef. Abbreviations as follows: Mat, maturity (M, fully mature; MBI, barely mature; I, immature); Sex, male or female; Distinguishing characteristics, 1–3, typical *N. pompilius* (1, umbilical callus; 2, color bands extend to umbilicus; 3, mottled, low-relief hood texture); 4–6, typical *N. stenomphalus* (4, open umbilicus, callus lacking; 5, umbilical area lacks color bands; 6, nodose hood texture). *Nautilus pompilius* possesses characteristics 1–3, *N. stenomphalus* 4–6. Intermediates (possible hybrids) are identified as *N. pompilius*? and *N. stenomphalus*? and lack one or more of the typical species shell characteristics (coloration or umbilical callus), but none identified as *N. pompilius* exhibits the roughly textured hood of *N. stenomphalus*. Thus, although there is some overlap in the shell characteristics, the combination of shell and hood characteristics appears to distinguish the two species.

	Spec. no.	Sex	Mat	Disting. char
I *N. pompilius*	1. Lz 1 (AM C 148212)	♀	M	1, 2, 3
	2. Lz 2 (USNM 816710)	♂	M	1, 2, 3
	3. Lz 8 (AM C 148216)	♂	M	1, 2, 3
	4. Lz 9	♂	M	1, 2, 3
	5. Lz 16	♂	MBI	1, 2, 3
	6. Lz 17	♀	M	1, 2, 3
	7. Lz 19	♂	M	1, 2, 3
	8. Lz 20	♂	MBI	1, 2, 3
	9. Lz 21	♂	M	1, 2, 3
	10. Lz 22	♂	M	1, 2, 3
	11. Lz 26	♂	M	1, 2, 3
II. *N. pompilius*?	1. Lz 5	?	I	1, 3, 5
	2. Lz 13	♀	MBI	1, 3, 5
III *N. stenomphalus*?	1. Lz 3 (USNM 816713)	♂	M	1, 5, 6
	2. Lz 4 (AM C 148215)	♂	MBI	1, 2, 6
	3. Lz 12	♂	M	1, 2, 6
	4. Lz 15	♂	M	1, 5, 6
	5. Lz 18	♂	MBI	1, 5, 6
	6. Lz 28	♂	I	1, 2, 6
	7. Lz 29	♂	M	1, 5, 6
	8. Lz 30	♂	M	1, 5, 6
	9. Lz 31	♂	M	1, 2, 6
IV *N. stenomphalus*	1. Lz 6 (USNM 816711)	♂	M	4, 5, 6
	2. Lz 7	♂	MBI	4, 5, 6
	3. Lz 10 (AM C 148211)	♂	M	4, 5, 6
	4. Lz 11	?	I	4, 5, 6
	5. Lz 23	♀	MBI	4, 5, 6
	6. Lz 24	♀	M	4, 5, 6
	7. Lz 25 (USNM 816712)	♂	M	4, 5, 6

questionable taxon; in fact, Saunders (1981) suggested that it might be a variant of *N. pompilius*, in which the callus was lacking, and the coloration reduced, as both features are known to occur separately in most populations of *N. pompilius*. But, as the Lizard Island specimens show, *N. stenomphalus* also has a distinctly textured hood. Thus, while *N. stenomphalus* is distinguishable from *N. pompilius*, it appears that in every case it might not be possible to separate them on the basis of shell characteristics alone; soft part morphology is also required.

Of the 11 Lizard Island "intermediates" (table 2; figure 2), two are regarded as representing *N. pompilius*?, because they show just one shell characteristic of *N. stenomphalus* (*e.g.*, a white umbilical area; table 2). Nine specimens identified as *N. stenomphalus*? show one or two shell characteristics of *N. pompilius* (a callus and/or umbilical color bands), but not the distinctive hood texture, which is here regarded as a characteristic of *N. stenomphalus* (table 2).

The presence of intermediate shell morphologies among the Great Barrier Reef specimens raises the possibility of hybridization between the two sympatric species; this is suggested for several reasons. First, the strongly textured hood of *N. stenomphalus* is truly unique; nothing like it has ever been recorded, either among the numerous populations of *N. pompilius* examined, or among the thousands of specimens of the morphologically similar species *N. belauensis*.

Second, reduced shell coloration and an open umbilicus are both features that have been observed in many populations of *N. pompilius* and in *N. belauensis*—in most cases they occur as a relatively rare variation and they have not been observed in the same specimen. However, no variant in these species has ever been observed in which the hood texture even approaches that of *N. stenomphalus*.

Third, the Lizard Island population does not appear to represent a random mixture of morphologies such as one might expect in a single, highly variable population;

rather, specimens seem to fall clearly into one distinctive category or the other, and the intermediates tend to show stronger affinities with either one or the other.

An alternative explanation for the intermediate morphologies is that the range of variability of *N. pompilius* is dramatically greater in the Queensland population than in any other documented occurrence of this widespread and well known species—enough so that it spans the accepted definition of two separate species. We do not favor this explanation, because (a) there has been no indication of such extremes in variation among the dozen or so populations of *N. pompilius* examined to date; and (b) not a single specimen of *N. pompilius* is known that exhibits the unique hood characteristics of the Lizard Island forms assigned to *N. stenomphalus*.

The Great Barrier Reef is only the second known site where more than a single species of *Nautilus* occurs sympatrically (see Saunders *et al.*, 1987). In addition, the occasional finds of drifted shells of the questionable species *N. repertus* Iredale, 1944 in this region (N. McKay, personal communication, 1985) suggest that three distinct species may inhabit the Great Barrier Reef, making this province the most speciose area known for *Nautilus*.

It is of interest to consider possible affiliations between the *Nautilus* found at Lizard Island and those from elsewhere in the region. The Great Barrier Reef Province is separated from the Papua New Guinea region by the narrow, shallow, Torres Straits. Because of the known distribution and locomotory habits of *Nautilus* (moving along the bottom, with maximum depths of approximately 600 m), the separation of Australia and Papua New Guinea by the Torres Straits would seemingly impose only an incomplete barrier to *Nautilus* migration between these two land areas. However, it would have been a formidable obstacle to migration from the west, particularly during the Pleistocene Epoch, when sealevel was as much as 120 m lower, as recently as 15,000 years ago.

Although the specimens of *N. pompilius* found at Lizard Island can, to some extent, be distinguished from representatives of this species captured at Port Moresby on the basis of coloration (Saunders & Davis, 1985; Swan & Saunders, 1987), the mature shells are the same size. In turn, the shells from these populations exhibit differences compared to larger morphs of *N. pompilius* found along the northern island groups of Papua New Guinea, such as Manus and New Ireland (Swan & Saunders, 1987). We suspect that the populations of *N. pompilius* occurring at Lizard Island and off southern Papua New Guinea are, or recently have been, part of a single, freely interbreeding population. Because of the prevailing north-to-south currents, however, gene flow and migration may be unidirectional from Papua New Guinea to the Great Barrier Reef. The absence of *N. stenomphalus* and *N. repertus* drift shells in southern Papua New Guinea may reflect this unidirectional dispersal, and suggest that the two latter forms are endemic to the Great Barrier Reef. The possible hybridization of *N. pompilius* with *N. stenomphalus* would suggest, according to this scenario, that *N. pompilius* and *N. stenomphalus* are sibling species, and that their recent sympatry is the result of *N. pompilius* expanding into the Great Barrier Reef Province.

ACKNOWLEDGEMENTS

The effort to study *Nautilus* on the Great Barrier Reef was undertaken with the approval of the Great Barrier Reef Marine Park Authority, and we thank R. A. Kenchington, D. W. Kinsey, and Wendy Craik for supporting the program. The project was based at the Lizard Island Research Station, where Dr. Barry Goldman, Director, provided invaluable advice and assistance. In addition, we are indebted to Lois Goldman, and to Gwen and Peter Pini, also of the Lizard Island Research Station, and Tom Landry, Seattle, Washington for their assistance. Bruce Carlson, Waikiki Aquarium, assisted in developing the effort to trap at Lizard Island. Mrs. N. McKay, of Cairns, Queensland, kindly made available for study drift shells of *Nautilus*, some of which matched Iredale's (1944) description of *N. repertus*. Supported by a U.S. National Science Foundation Grant (EAR 83-18932) and by the National Geographic Society.

LITERATURE CITED

Cotton, B. C. 1957. Records of uncommon southern Australian molluscs. Records South Australian Museum 13:117–130.

Iredale, T. 1944. Australian pearly nautilus. Australian Zoologist 10:294–298.

Riddle, A. R. 1920. An adventitious occurrence of *Nautilus pompilius*, Linne, with a short bibliography on ocean currents affecting the Australian coast. Transactions Royal Society South Australia 44:257–262.

Saunders, W. B. 1981. The species of living *Nautilus* and their distribution. The Veliger 24:8–17.

Saunders, W. B. 1987. The species of *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London, p. 35–52.

Saunders, W. B. and L. E. Davis. 1985. A preliminary report on *Nautilus* in Papua New Guinea. Science in New Guinea 11:60–69.

Saunders, W. B., L. E. Davis, and R. L. Knight. 1987. Sympatric species of *Nautilus* (*N. pompilius* and *N. scrobiculatus*) in the Admiralty Islands, Papua New Guinea. The Nautilus 101:93–99.

Saunders, W. B. and P. D. Ward. 1987. Ecology, distribution, and population characteristics of *Nautilus*. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London, p. 137–162.

Sowerby, G. B. 1849. Monograph on the genus *Nautilus*. Thesaurus Conchyliorum 2:463–465.

Swan, A. R. H. and W. B. Saunders. 1987. Morphologic variation in *Nautilus* from Papua New Guinea. *In:* Saunders, W. B. and N. H. Landman (eds.). *Nautilus*: the biology and paleobiology of a living fossil. Plenum Press, New York and London, p. 85–103.

On the Availability of Names Proposed in *Pacific Shell News*, Tokyo, 1970–72

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ABSTRACT

The nomenclatural status of two genus-group names and 19 species-group names described in *Pacific Shell News*, Numbers 1–3 (1970) and 5, 6 (1972) are critically reviewed. The following taxa are available names under provisions of the International Code of Zoological Nomenclature. SPECIES-GROUP NAMES: In Number 1 (January 20, 1970): *Conus memiae* Habe and Kosuge; *Claviscala midwayensis* Habe and Kosuge. In Number 2 (April 30, 1970): *Cypraea* (*Erosaria*) *miyokoae* Habe and Kosuge; *Clavus regius* Habe and Murakami; *Fulgoraria glabra* Habe and Kosuge; *Ctenocardia kinai* Habe and Murakami; *Conus kintoki* Habe and Kosuge. In Number 3 (October 30, 1970): *Phyllocoma neglecta* Habe and Kosuge; *Typhis ramosus* Habe and Kosuge; *Ginebis corolla* Habe and Kosuge; *Conus spirofilis* Habe and Kosuge. In Number 5 (September 5, 1972): *Cornutoconus lamellatus* Suzuki; *Homalopoma striatum* Suzuki. In Number 6 (December 1, 1972): *Latiaxis* (*sensu stricto*) *longispinosus* Suzuki; *Latiaxis* (*Babelomurex*) *pagodus pervernicosus* Suzuki. GENUS-GROUP NAME: In Number 5 (September 5, 1972): *Cornutoconus* Suzuki.

INTRODUCTION

Pacific Shell News (1970 and 1972) was intended as a popular magazine to promote the hobby of shell collecting to the Japanese audience. The first three numbers (1970), under the co-editorship of Drs. Tadashige Habe and Sadao Kosuge, are well illustrated with numerous monochrome and a few polychrome photographs. The text, including the illustrations, consists of about 40 pages per issue; it is mostly in Japanese, but has brief passages in English for some of the species discussed. One of the features of each issue was to provide a notice of forthcoming descriptions of new generic and specific taxa which were to be published in *Venus (Japanese Journal of Malacology)* or *The Nautilus*. Not all of the intended descriptions of new taxa by these authors, however, appeared elsewhere in print.

It was not the intent of the authors of these descriptions to propose new taxa in this popular magazine (Taki and Habe, 1973:161). Nevertheless, their actions, though inadvertent, constituted nomenclatural acts under the provisions of the International Code of Zoological Nomenclature (ICZN, 1985, Articles 1 and 10–20) that resulted in some of these taxa being validly proposed in these first three numbers. Various workers have accepted, rejected, or ignored the availability of the names validly proposed in this magazine (Emerson, 1984; Coomans *et al.*, 1985; Coomans, 1986).

As a result of conflicting views concerning the availability of the new generic and specific taxa described in Numbers 1–3 of *Pacific Shell News*, we have undertaken a review of the nomenclatural status of these commonly overlooked taxa. It is beyond the scope of this paper for us to determine the correct scientific name (valid name, ICZN, 1985, Article 23a) for these taxa.

For completeness we have also included a review of taxa proposed by Masaji Suzuki in Numbers 5 and 6 (No. 4 was not issued; Sadao Kosuge, *in litt.*, October 14, 1986), for some of these taxa are largely unknown to workers owing to the rarity of the last two issues of *Pacific Shell News* (1972).

The following abbreviations are used in the text: ICZN = International Code of Zoological Nomenclature; IMT = Institute of Malacology, Tokyo; NSMT = National Science Museum, Tokyo.

In the Japanese text, scientific names were latinized unless indicated to have been derived from Japanese ideograms. In the case of nominal species for which the holotype was only illustrated in *Pacific Shell News*, we have reproduced the original illustrations.

NOMENCLATURAL STATUS

Taxa Considered in Number 1, January 20, 1970

Pacific Shell News, Number 1, i–iii + 41 pages; frontispiece in color, 18 photographs in black and white. Date of publication not given in this issue. Inaba and Oyama (1977) gave the date for the taxa cited by them in this number as January 20, 1970. Despite the fact that Taki (1970:80) noted that he had received his copy on March

1, 1970, Dr. Kosuge confirmed (*in litt.*, February 19, 1985) January 20, 1970 as the actual date of publication.

1. *Conus coralinus* Habe and Kosuge, p. i (color frontispiece), ii (Japanese text) (Conidae). This taxon was briefly discussed in the caption to the photograph. There is no indication that the authors proposed to describe this as a new species here or elsewhere; a *nomen nudum*.

Nomenclatural status: Not available here. Validly proposed as *Rhizoconus coralinus* Habe and Kosuge, 1970c. NOT *Conus corallinus* Kiener, 1845. Considered a junior synonym of *C. klemae* (Cotton, 1953) by Walls (1979: 626, 627, 401) and Coomans *et al.* (1985:261). *Conus coralinus* (Habe and Kosuge, 1970) is a junior homonym of *C. corallinus* Kiener, 1845 (see Coomans *et al.*, 1985).

2. *Latiaxis* (*Lamellatiaxis*) Habe and Kosuge, p. 7 (Coralliophilidae). A diagnosis for a new genus-group name was not provided for *Lamellatiaxis*; a *nomen nudum*.

Nomenclatural status: Not available here. *Lamellatiaxis* was validly proposed as a new subgenus by Habe and Kosuge (1970a:182), type species by original designation: *Latiaxis* (*Lamellatiaxis*) *marumai* Habe and Kosuge, 1970. Kosuge and Suzuki (1985:23) subsequently placed *Lamellatiaxis* as a subgenus in the genus *Babelomurex* Coen, 1922.

3. *Latiaxis* (*Lamellatiaxis*) *marumai* Habe and Kosuge, p. 7, 2 figs. (Coralliophilidae). The description of the species-group name *L.* (*L.*) *marumai* Habe and Kosuge, 1970 in this number lacks a statement in the text that can satisfy the requirement to differentiate the species [ICZN, 1985, Article 13a(i)]; a *nomen nudum*.

Nomenclatural status: Not available here. Validly proposed as *Latiaxis* (*Lamellatiaxis*) *marumai* Habe and Kosuge, 1970a. Kosuge and Suzuki (1985:24) dated the availability of this taxon from the description in *Venus*.

4. *Conus memiae* Habe and Kosuge, p. 8, 2 figs., holotype (Conidae). Text in Japanese compares this new species with *C. japonicus* (name in Japanese ideograms) and *C. wakayamaensis* (name in Japanese ideograms) and morphologically differentiates this taxon.

Nomenclatural status: Available here. Subsequently proposed as *Asprella memiae* Habe and Kosuge, 1970c. Kohn and Riggs (1979:140) dated the availability of this taxon from *Pacific Shell News*, Number 1. Walls (1979: 706) considered *Conus* (*Asprella*) *adonis* Shikama, 1971, to be a junior synonym of this species.

5. *Galeoastraea midwayensis* Habe and Kosuge, p. 9, 3 figs. (Turbinidae). Neither the Japanese nor English text makes a statement that purports to differentiate this "new species"; a *nomen nudum*.

Nomenclatural status: Not available here. Validly proposed as *Galeoastraea midwayensis* Habe and Kosuge, 1970d.

6. *Claviscala midwayensis* Habe and Kosuge, p. 10, 1 fig., holotype (Epitoniidae). The Japanese text compares this "new species" with *C. kuroharai* (name in Japanese ideograms) and morphologically differentiates this taxon.

Nomenclatural status: Available here. Subsequently proposed as *Claviscala midwayensis* Habe and Kosuge, 1970d.

Taxa Considered in Number 2, April 30, 1970

Pacific Shell News, Number 2, i–iii + 40 pages, frontispiece in color, 18 photographs in black and white. Date of publication April 30, 1970, indicated on inside of back cover; date verified by Inaba and Oyama (1977).

1. *Cypraea* (*Erosaria*) *miyokoae* Habe and Kosuge, p. i (color frontispiece; dorsal and apertural views of holotype), ii (Japanese text) (Cypraeidae). The brief explanation in Japanese to the figures states in part "Unlike ordinary *Cypraea tigris* [name in Japanese ideograms], this species is characterized by its scattered color dots which become darker and finer along the edge. And as it matures, the beaks at both ends become a beautiful purple-red. It was found in the South China Sea and was purchased in Taiwan. . . . We named ours [this species] in honor of the collector, Mr. Suzuki's wife." In English: "Measurement: 41.5 × 27.0 mm." The description, although admittedly brief, compares this taxon with *Cypraea tigris* Linnaeus and purports to differentiate this species.

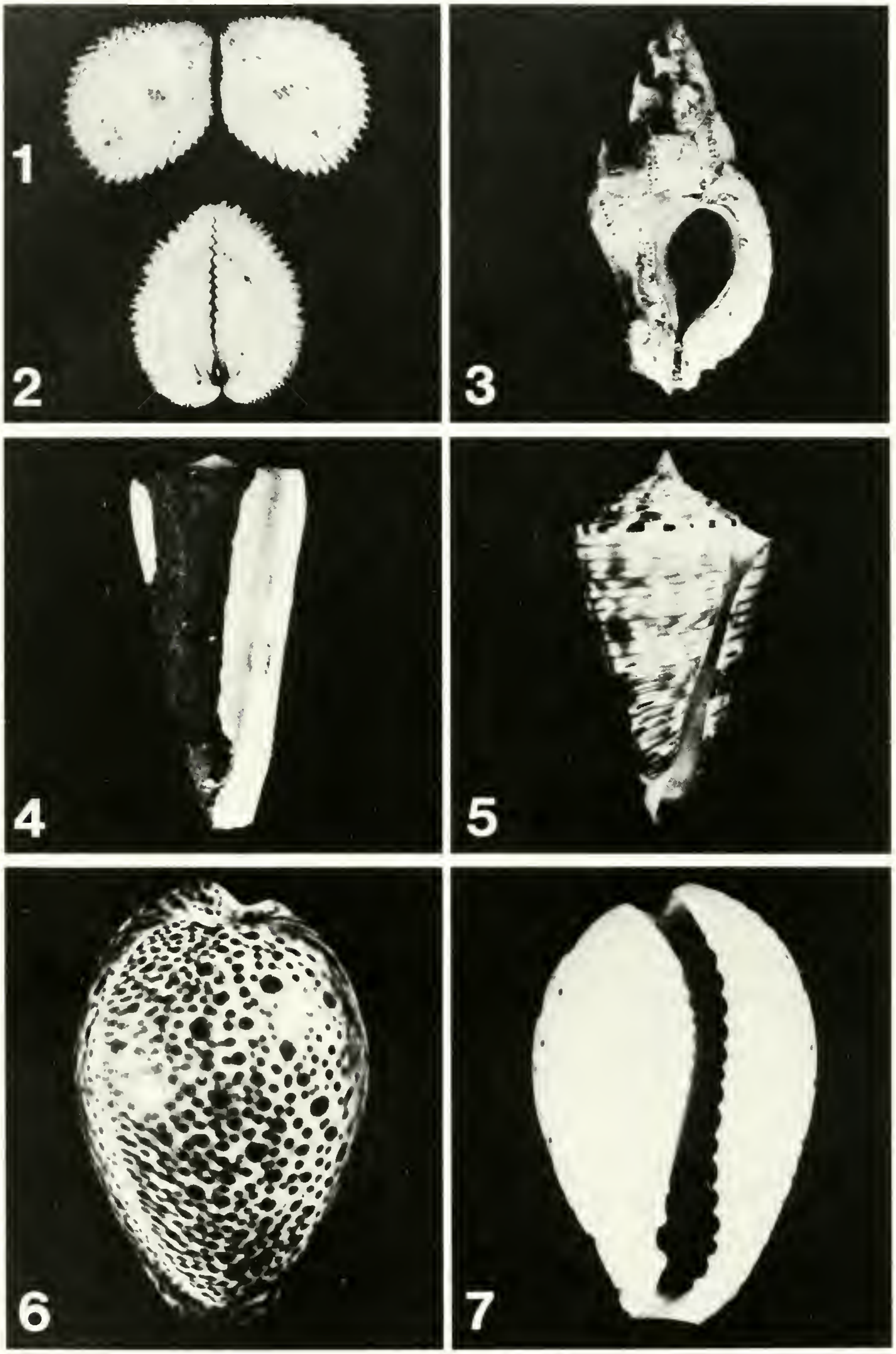
Nomenclatural status: Available here. Inaba and Oyama (1977:78) cited this taxon as a manuscript name, "name and figure only." On the other hand, Burgess (1985:271, pl. 20, c, not holotype) considered this taxon to be an available name. Burgess (1985) stated that he examined the holotype and he referred this taxon to the synonymy of *C. turdus* Lamarck, 1810, but we question the locality data, "Bashi Channel," cited by Burgess. The apparently mislocalized data were provided by a Taiwanese shell dealer from whom the specimen was purchased. The depository of the holotype has not been determined, the original illustrations are reproduced here (figures 6, 7).

2. *Clavus regius* Habe and Murakami, p. 6, 2 figs., holotype (Turridae). The Japanese text states the new species is referable to the Turridae and briefly discusses some turrid genera. The English text repeats in part the description of the Japanese text: "This is the largest species belonging to the genus *Clavus* and collected from the Ryukyu mainland by Mr. Kina, the keen collector in Okinawa. The shell is solid and light [red-]brown with a series of [charcoal-]brown nodules on the whorls. . . . Measurement: 54.5 × 23.3 mm." The description fulfills the provisions of the Code requiring a statement purporting to differentiate a new species.

Nomenclatural status: Available here. The holotype (NSMT-Mo 53139) was illustrated by Inaba and Oyama (1977:101, pl. 7, fig. 11), who also mentioned the presence of two paratypes (NSMT-Mo 53143 and 53144).

3. *Fulgoraria glabra* Habe and Kosuge, p. 7, 2 figs., holotype (Volutidae). Text in Japanese compares this new species to *F. leviuscula* Rehder, 1969 and morphologically differentiates this taxon.

Nomenclatural status: Available here. Subsequently



Figures 1–7. Reproductions of original illustrations; × 1. **1, 2.** *Ctenocardia kinai* Habe and Murakami, 1970. **3.** *Phyllocoma neglecta* Habe and Kosuge, 1970. **4.** *Conus kintoki* Habe and Kosuge, 1970. **5.** *Conus spirofilis* Habe and Kosuge, 1970. **6, 7.** *Cypraea* (*Erosaria*) *miyokoae* Habe and Kosuge, 1970

proposed as *Fulgoraria* (*Fulgoraria*) *glabra* Habe and Kosuge, 1970b.

4. *Ctenocardia kinai* Habe and Murakami, p. 8, 2 figs., holotype (Cardiidae). The Japanese text compares this taxon with *C. symbolica* Iredale, 1928 and *C. perornata* Iredale, 1928. The English text states in part, "This new porcupine cockle has been brought from the Ryukyu mainland. . . . This is recognized by the snowy white shell scattered flesh orange blotches and armed by the spiny ribs of about thirty-two in number. *Ct. symbolica* Iredale from the Philippines is the most closely allied species to this new species. . . . Measurement: 54.0 × 43.0 mm."

Nomenclatural status: Available here. Inaba and Oyama (1977:62) recorded the presence of the holotype, NSMT-Mo 53149 and a paratype, NSMT-Mo 53150. The original illustrations are reproduced here (figures 1, 2). *Ctenocardia victor* (Angas, 1872) is a senior synonym of *C. kinai* Habe and Murakami, 1970, a taxonomic placement confirmed by Dr. Habe (*in litt.*, April 29, 1987).

5. *Conus kintoki* Habe and Kosuge, p. 9, 1 fig., holotype (Conidae). The status of this taxon was previously discussed by the senior author and accepted as a validly proposed name (Emerson, 1984). Inaba and Oyama (1977: 63) stated that the holotype (102.0 × 49.5 mm) is deposited in the collection of Dr. Kosuge. We have been informed by Dr. Kosuge that the holotype is neither in his collection nor that of Mr. Masaji Suzuki (*in litt.*, October 14, 1986 and March 10, 1987). The original illustration is reproduced here (figure 4).

Nomenclatural status: Available here. Kohn and Riggs (1979:139) dated the availability of this taxon from *Pacific Shell News*, Number 2. *Conus kintoki* Coomans and Moolenbeek (1982:136, 137, fig. 4) is a junior subjective synonym of this taxon, as pointed out by Emerson (1984: 59).

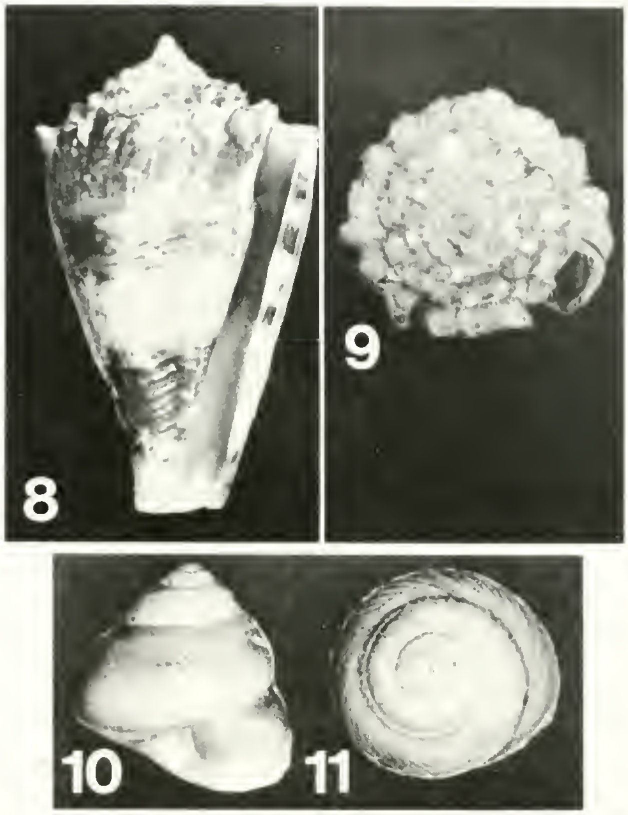
6. *Conus* (*Parviconus*) *nadaensis* Azuma and Toki, p. 30, 2 figs. (Conidae). The Japanese text is largely devoted to an announcement of the independent discoveries of this new cone from off Kii, Japan by Koji Nomoto and by Masao Azuma and Raisaburo Toki. These newly found specimens were not compared with other species and no attempt was made to differentiate this species; a *nomen nudum*.

Nomenclatural status: Not available here. Validly proposed as *Endemnoconus* [*sic*] *nadaensis* Azuma and Toki, 1970.

Taxa Considered in Number 3, October 30, 1970

Pacific Shell News, Number 3, i–iii + 38 pages, frontispiece in color, 26 photographs in black and white. Date of publication: October 30, 1970, indicated on inside of back cover.

1. *Phyllocoma neglecta* Habe and Kosuge, p. 7, 1 fig., holotype (Muricidae). An English translation of the Japanese text and other data relating to the proposal of this taxon were presented by Emerson and D'Attilio (1979: 1, 2, figs. 17, 18, Philippine specimen) and need not be repeated here, as the description is validly proposed under the provisions of the Code.



Figures 8–11. Reproductions of original illustrations; × 1. **8, 9.** *Cornutoconus lamellatus* Suzuki, 1972. **10, 11.** *Homalopoma striatum* Suzuki, 1972.

Nomenclatural status: Available here. This taxon is referred to the genus *Dermomurex* Monterosato, 1890 by Emerson and D'Attilio (1979) and by Vokes (1985: 47, pl. 1, figs. 7a,b). Inaba and Oyama (1977:82) stated that the holotype (22.5 × 11.2 mm) is deposited in the collection of Dr. Kosuge. We have been informed by Dr. Kosuge that the holotype is neither in his collection nor that of Mr. Masaji Suzuki (*in litt.*, October 14, 1986 and March 10, 1987). The original illustration is reproduced here (figure 3).

2. *Typhis ramosus* Habe and Kosuge, p. 8, 2 figs. (Muricidae). The Japanese text discusses the typhid species known from Japan and describes this new species from the South China Sea as follows: shell solid, color light brown with darker spiral lines; varices four, sculptured with sharp spines and hollow projections, the terminal pipe being the largest and protruding laterally and slightly upward. The new species is compared with *T. philipensis* [*sic*] Watson [= *Typhina philippensis* (Watson, 1883)].

Nomenclatural status: Available here. Subsequently proposed as *Typhis ramosus* Habe and Kosuge, 1971 (holotype, NSMT-Mo 38872). The original description was partially repeated in 1973 [*Hawaiian Shell News*

21(11):11, 2 figs.]. Inaba and Oyama (1977:103, pl. 6, fig. 6) also illustrated the holotype and recorded a paratype, NSMT-Mo 39016).

3. *Ginebis corolla* Habe and Kosuge, p. 10, 1 fig., holotype (Trochidae). The Japanese text discusses the distribution of regional species of *Ginebis* and compares this new species with them. The English text states: "This new species differs from the other two related forms in Japan (*G. argenteonitens* and *G. hirasei*) in its broader shell width, beaded granules of each whorl and number of spiral threads on the base of body whorl. The [two] specimens were collected from the South China Sea at a depth of about 200 m[eters]. . . . Measurement: 49.5 × 39.5 mm."

Nomenclatural status: Available here. Inaba and Oyama (1977:33, pl. 6, fig. 3) illustrated the holotype (NSMT-Mo 45547). Subsequently described as *Ginebis hamadai* Kosuge, 1980 (holotype, IMT-80-5).

4. *Conus spirofilis* Habe and Kosuge, p. 11, 1 fig., holotype (Conidae). The Japanese text compares this new species with *C. hirasei* and morphologically differentiates this taxon. The English text states: "This pretty new cone shell was collected from the South China Sea and more than five specimens had been brought to Japan. It is easily distinguished [from *C. hirasei* (Kira)] for its spiral color striae, dark brown color bands and irregular white patches. . . . Measurement: 30.8 × 16.7 mm."

Nomenclatural status: Available here. Inaba and Oyama (1977:116) and Kohn and Riggs (1979:144) dated the availability of this taxon from *Pacific Shell News*, Number 3. Inaba and Oyama (1977) stated that the holotype is deposited in the collection of Dr. Kosuge. We have been informed by Dr. Kosuge that the holotype is neither in his collection nor that of Mr. Masaji Suzuki (*in litt.*, October 14, 1986 and March 10, 1987). The original illustration is reproduced here (figure 5).

Validly Proposed Taxa in Number 5, September 5, 1972, in "Descriptions of Two New Species of Gastropods" by [Masaji] Suzuki

Pacific Shell News, Number 5, four unnumbered pages, two black and white photographs. Date of publication: indicated on fourth page as May 31, 1972. However, the actual date of publication was September 5, 1972 (Kosuge, 1985:4). In the Japanese text on the fourth page, Masaji Suzuki stated that Number 5 was being sent as a combined issue for Numbers 4 and 5. It should be noted that the Pacific Shell Club, in May, 1971, sponsored an exhibition of shells in Tokyo and issued on this occasion an illustrated catalog pertaining to the shells on display. No new taxa were proposed in this catalog, "Jewels of the Sea: Seashells of the World." This publication cannot be construed to be *Pacific Shell News*, Number 4, which was never published (Kosuge, *in litt.*).

1. *Cornutoconus* Suzuki, first and second pages, type species by original designation, *Cornutoconus lamellatus* Suzuki, 1972. For taxonomic status, see remarks below

2. *Cornutoconus lamellatus* Suzuki, second page, text fig. 1 (two views of holotype) (Conidae). Type locality: off Sumisu Isle, near Hachijo Id., Izu Islands, in about 300 meters, South China Sea. The holotype (18.4 × 11.0 mm) and a paratype (16.7 × 8.7 mm) from the Maruma Collection are stated to have been deposited in the NSMT. The original illustrations are reproduced here (figures 8, 9).

Remarks: According to Taki and Habe (1973:161), Coomans *et al.* (1983:114), and Kosuge (1985:4), *Cornutoconus lamellatus* Suzuki, 1972 is a junior synonym of *Taranteconus chiangi* Azuma, 1972. Consequently, *Cornutoconus* Suzuki, 1972 is also a junior synonym of *Taranteconus* Azuma, 1972, because the type species by original designation is *Taranteconus chiangi* Azuma, 1972. Therefore, *Taranteconus* and *T. chiangi* have priority over *Cornutoconus* and *C. lamellatus*, respectively.

3. *Homalopoma striatum* Suzuki, third page, text fig. 2 (three views) (Turbinidae). Type locality: same as for *Cornutoconus lamellatus*. The holotype (12.2 × 11.4 mm) and a paratype (11.2 × 10.6 mm) from the Maruma collection are stated to have been deposited in the NSMT. The original illustrations are reproduced here (figures 10, 11).

Remarks: According to Taki and Habe (1973:161) and Dr. Sadao Kosuge (*in litt.*, February 19, 1985), *Homalopoma striatum* Suzuki, 1972 is a junior synonym of *H. eoa* Azuma, 1972.

Validly Proposed Taxa in Number 6, December 1, 1972, in "Descriptions of New Species of *Latiaxis*" by Masaji Suzuki (first three pages)

Pacific Shell News, Number 6, four unnumbered pages, two black and white photographs. Date of publication: indicated on fourth page as December 1, 1972.

1. *Latiaxis* (*sensu stricto*) *longispinosus* Suzuki, first and second pages, text fig. (two views of holotype) (Coralliophilidae). Type locality: off Onna, Okinawa Main Island, Okinawa Pref., Japan. The holotype (32.4 × 39.6 mm) from the Suzuki Collection is deposited in the IMT (85-17) (*fide* Kosuge & Suzuki, 1985:15).

Remarks: Kosuge and Suzuki (1985:15) referred this taxon to the genus *Babelomurex* Coen, 1922, and considered it a senior synonym of *Latiaxis pisori* D'Attilio and Emerson, 1980. Mr. D'Attilio and one of us (W.K.E.) afford *L. pisori* full specific status on the basis of morphological differences of the spire and spines of these two nominal species (see D'Attilio, 1985:98–100, figs. 1–4, for additional comments on *L. pisori*).

2. *Latiaxis* (*Babelomurex*) *pagodus pervernicosus* Suzuki, second and third pages, text fig. (holotype and paratype) (Coralliophilidae). Type locality: off Ogasawara Islands (Bonin Ids.), in 200 meters. The holotype

(23.5 × 22.3 mm) from the Suzuki Collection is deposited in IMT (85-18) (*fide* Kosuge & Suzuki, 1985:16).

Remarks: Kosuge and Suzuki (1985) raised this taxon to full specific standing in the genus *Babelomurex*.

ACKNOWLEDGEMENTS

We are greatly indebted to Ms. Nancy Broschart for contributing an English translation of pertinent passages of the Japanese texts. Without her enthusiastic cooperation we could not have undertaken this review. Mr. Masao Tabakotani generously provided a translation of relevant pages of the catalog for the 1971 shell exhibition. We thank Dr. Sadao Kosuge for generously providing us with original copies of *Pacific Shell News* and for answering numerous questions regarding its publication. We also thank Dr. Tadashige Habe for his informative correspondence on this subject.

LITERATURE CITED

Azuma, M. 1972. Descriptions of four new gastropods from South China Sea. Venus 31(2):55–61, 10 figs. (July 30).

Azuma, M. and R. Toki. 1970. Description of a new cone from Kii Peninsula, Honshu. Venus 29(3):77–80, 4 figs. (Aug. 31).

Burgess, C. M. 1985. Cowries of the world. Seacomber Publications, Cape Town, i–XVII + 289 p., illus.

Coomans, H. E. 1986. Old and new names in the Conidae. Hawaiian Shell News 34(10):7, 8, 3 figs.

Coomans, H. E. and R. G. Moolenbeek. 1982. Studies on Conidae (Mollusca, Gastropoda) 1. *Conus papuensis* and *C. kintoki*, two new species from deeper water in the western Pacific. Bulletin Zoologisch Museum Universiteit van Amsterdam 8(15):133–138, 6 figs.

Coomans, H. E., R. G. Moolenbeek, and E. Wils. 1983. Alphabetical revision of the (sub)species in Recent Conidae. 6. *cabritii* to *cinereus*. Basteria 47(5–6):67–143, figs. 293–430.

Coomans, H. E., R. G. Moolenbeek, and E. Wils. 1985. Alphabetical revision of the (sub)species in Recent Conidae. 7. *cingulatus* to *cylindraceus*, including *Conus shikamai nomen novum*. Basteria 48(6):223–311, figs. 431–581.

D'Attilio, A. 1985. A note on *Latiaxis pisori* D'Attilio and Emerson, 1980. The Festivus (San Diego Shell Club) 17(10): 98–100, 4 figs.

Emerson, W. K. 1984. *Conus kintoki* Habe and Kosuge, 1970: a validly proposed taxon. The Nautilus 98(2):58–60, 3 figs.

Emerson, W. K. and A. D'Attilio. 1979. Six new species of muricacean gastropods. The Nautilus 93(1):1–10, 18 figs.

Habe, T. and S. Kosuge. 1970a. Description of new subgenus and species of *Latiaxis* from the South China Sea. Venus 28(4):182–185, 3 figs. (Jan. 31).

Habe, T. and S. Kosuge. 1970b. Description of new species of *Fulgoraria* from the South China Sea. Venus 29(1):1–3, 2 figs. (May 15).

Habe, T. and S. Kosuge. 1970c. Descriptions of two new species of cone shell from the Philippines and Taiwan. Venus 29(3):81–83, pl. 5 (Aug. 31).

Habe, T. and S. Kosuge. 1970d. Descriptions of three new gastropods from the sea around Midway. Venus 29(3):87–91, pl. 6 (Aug. 31).

Habe, T. and S. Kosuge. 1971. New typhid species from South China Sea. The Nautilus 84(3):82–83, 2 figs. (Jan. 25). [Article partially reprinted in Hawaiian Shell News 21(11): 11, 2 figs., 1973.]

Inaba, T. and K. Oyama. 1977. Catalogue of molluscan taxa described by Tadashige Habe during 1939–1975, with illustrations of hitherto unfigured species. Tokyo, 184 p., 7 pls.

International Commission on Zoological Nomenclature. 1985. International code of zoological nomenclature, 3rd ed. London, xx + 338 p.

Kohn, A. J. and A. C. Riggs. 1979. Catalogue of Recent and fossil *Conus*, 1937–1976. The Journal of Molluscan Studies 45(1):131–147.

Kosuge, S. 1980. Description of new species of the genus *Ginebis* from the South China Sea (Trochidae, Gastropoda). Bulletin of the Institute of Malacology Tokyo 1(3):40, pl. 9, figs. 1–3.

Kosuge, S. 1985. *Chiangi* or *lamellatus*? Hawaiian Shell News 33(8):4.

Kosuge, S. and M. Suzuki. 1985. Illustrated catalogue of *Latiaxis* and its related groups. Family Coralliophilidae. Institute of Malacology of Tokyo, Special Publication No. 1, 83 p., 50 pls.

Rehder, H. A. 1969. New species and subgenera of Volutidae (Fulgorariinae) from the South China Sea and Japan. Venus 27(4):127–132, pl. 7.

Shikama, T. 1971. On some noteworthy marine Gastropoda from southwestern Japan (III). Science Reports of the Yokohama National University (II), 18:27–35, pl. 3, 2 text figs.

Taki, I. 1970. [Notes on Pacific Shell Club.] Venus 29(3):80 (Aug. 31).

Taki, I. and T. Habe. 1973. [Review and Abstract.] Venus 31(4):161 (Jan. 30).

Vokes, E. H. 1985. The genus *Dermomurex* (Mollusca: Gastropoda) in Australia. Journal of the Malacological Society of Australia 7(1–2):45–65, 3 pls.

Walls, J. G. 1979. Cone shells, a synopsis of the living Conidae. T.F.H. Publications, Inc., Neptune City, NJ, 1011 p., illus.

A New *Ecphora* Fauna from Southern Florida

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ABSTRACT

A species radiation of the extinct rapanine thaidid genus *Ecphora* Conrad, 1843 is reported from the lowermost beds of the Pliocene Buckingham Formation (= Pinecrest Beds of Olsson) at Sarasota, Florida. Five *Ecphora* species were collected together in the basal units (Units 10 and 11 of Petuch, 1982) of the Macasphalt Newburn Pit Mine, and these constitute the richest *Ecphora* fauna ever reported from one locality. Of these five species, three were previously described. *Ecphora quadricostata* (Say, 1824) and *E. parvicostata* Pilsbry, 1911, which range from Virginia to Florida, and *E. striatula* Petuch, 1986, which is confined to southern Florida. Two species, *E. bradleyae* and *E. hertweckorum*, are described as new.

INTRODUCTION

In the late 1960's, a new molluscan paleontological resource opened near Sarasota, Florida. This site, the Macasphalt Newburn Pit Mine #0800826 (formerly the "Warren Brothers Shell Pit") is dug entirely into the Pliocene Buckingham Formation (Mansfield, 1939; = Pinecrest Beds of Olsson, 1968; Petuch, 1986). This locality has proven to be one of the most important paleontological collection areas in peninsular Florida. The pit mine is unusual for Florida because of its large size and in that it is continuously pumped, preventing filling by groundwater and allowing for in-place collecting down to 70 foot depths (21 m). The remarkable richness of the Sarasota molluscan fauna far surpasses that of any other known Pliocene fauna in the eastern United States. To date, I have collected over 600 species of gastropods from the quarry, of which at least half are estimated as being new to science (Petuch, 1982).

A preliminary survey of the faunas and stratigraphy of the Macasphalt Pit Mine has shown that there are 11 fossiliferous beds or members exposed in the quarry. A stratigraphic arrangement of numbered units, starting at the top and working downward (since the quarry is being deepened), was given in my earlier paper on the Sarasota pit mine (Petuch, 1982). The upper beds (Units 1–9) contain a typical, although extremely rich, warm water Pliocene fauna that has many elements in common with the upper beds of the Yorktown Formation of Virginia and northern North Carolina, the Duplin Formation of the Carolinas, and the upper bed of the Jackson Bluff Formation of northwestern Florida (the "*Cancellaria* Zone" of Mansfield, 1930). These formations have been shown to be contemporaneous (Hazel, 1983). The basal beds of the quarry (Units 10 and 11), however, contain a very different molluscan assemblage with several species of the extinct rapanine thaidid genus *Ecphora* Conrad, 1843. The fauna of these lowermost units resembles those of the lower beds of the Yorktown Formation and the "*Ecphora* Zone" of the Jackson Bluff Formation (Mansfield, 1930).

Unlike the northern Florida Pliocene beds, which most often contain a single, often poorly preserved, species of *Ecphora*, the basal units of the Buckingham Formation at Sarasota contain a well-preserved and richer fauna. Altogether, five species have been collected from these lower units. This is the richest single *Ecphora* fauna presently known from any formation, surpassing that of the Miocene beds of Chesapeake Bay. The five species of the Buckingham Formation may possibly represent the last *Ecphora* species radiation; the "last gasp" of a group that died out at the end of the Pliocene.

In this paper, the Sarasota *Ecphora* radiation is described for the first time, as are two new *Ecphora* species. Institutional abbreviations used here include: USNM (National Museum of Natural History, Smithsonian Institution, Washington, D.C.); MCZ (Museum of Comparative Zoology, Harvard University).

SYSTEMATICS

Family **Thaididae**
Subfamily **Rapaninae**
Genus *Ecphora* Conrad, 1843

Ecphora quadricostata (Say, 1824)
(figures 10–12)

Fusus 4-costatus Say, 1824 127, pl. vii, fig. 5.
Fusus quadricostatus Conrad, 1830:211.
Ecphora quadricostata Conrad, 1843:310
Colus quadricostatus Tuomey and Holmes, 1857:149, pl. xxx, fig. 4
Ecphora quadricostata umbilicata (Wagner) Mansfield, 1930: 70–71, pl. 17, fig. 7.

Ecphora quadricostata Olsson, 1968:73–75, pl. 1, fig. 1.
Ecphora quadricostata Wilson, 1987:23–25.

Material examined: Two specimens, lengths 30 mm and 52 mm (incomplete), Unit 11 of Macasphalt Pit Mine #0800826, Sarasota, Florida, paleontology collection of Department of Geology, Florida Atlantic University; length 29 mm, spoil pile from construction dig, Cape Coral, Lee County, Florida, MCZ 29453 (figures 11, 12); length 60 mm, Unit 11 of Macasphalt Newburn Pit Mine, Petuch collection.

Discussion: Although *Ecphora quadricostata* is common in the Yorktown and Duplin formations, it is relatively rare in southern Florida, with only one previous pictorially documented example (Olsson, 1968: pl. 1, fig. 1). The paucity of specimens of *E. quadricostata* in southern Florida may reflect paleotemperature preferences, with *E. quadricostata* having preferred the cooler water temperatures of the mid-Atlantic region and the closely-related *E. hertweckorum* new species and *E. striatula* Petuch, 1986 having preferred the tropical lagoonal and coral reef environments of peninsular Florida.

Ecphora quadricostata differs from its Floridian relatives, *E. hertweckorum* and *E. striatula*, in being stockier and heavier, with small but noticeable "T"-shaped flanges on the ribs (figure 19). Specimens examined from Virginia, North Carolina, and Florida, all had one or two grooves on each rib. These grooves, which are arranged medially, give the rib a bisected appearance. The closely-related *E. hertweckorum* lacks these grooves. Occasional specimens of *E. quadricostata* show a fifth, smaller rib around the base of the siphonal canal, but this fifth rib is never equal in size to the other ribs.

Wilson (1987) recently resolved some of the taxonomic problems revolving around *E. quadricostata*. He demonstrated unequivocably that *E. quadricostata* is a Pliocene species, typically from the Yorktown Formation, and that the Maryland Miocene species referred to this taxon by Martin (1904) was actually a new species, which he named *E. gardnerae*. Wilson also showed that the taxon *E. quadricostata umbilicata* "Wagner" (of authors), often applied to Floridian specimens of *E. quadricostata* (*i.e.*, Mansfield, 1930), is a synonym of *E. quadricostata*.

Ecphora parvicostata Pilsbry, 1911
(figures 8, 9)

Ecphora parvicostata Pilsbry, 1911:438–439, Wilson, 1987:23

Material examined: Two specimens, lengths 92 mm and 30 mm (juvenile), Unit 11 of Macasphalt Pit Mine #0800826, Sarasota, Florida, MCZ 29452; length 101 mm (figured here), same locality, Petuch collection.

Discussion: *Ecphora parvicostata* has the most inflated shell and least developed ribs of the known Floridian *Ecphora* species. In cross section (figure 16), the ribs are rounded in shape and are adherent to the body whorl. As in *E. quadricostata*, the ribs of *E. parvicostata* also are marked with a medial groove, giving the rib a bisected appearance. Unlike *E. quadricostata*, *E. parvicostata* is an intricately sculptured species when young, becoming smoother and less sculptured as it matures. The 30 mm juvenile specimen listed above (MCZ 29452) has numerous large spiral cords and intermittent pitlike depressions between the ribs. The shoulder of the juvenile *E. parvicostata* is also distinctly rounded. Conversely, the 29 mm juvenile *E. quadricostata* listed previously (MCZ 29453) is smooth between the ribs, as in adults, and has an angled shoulder.

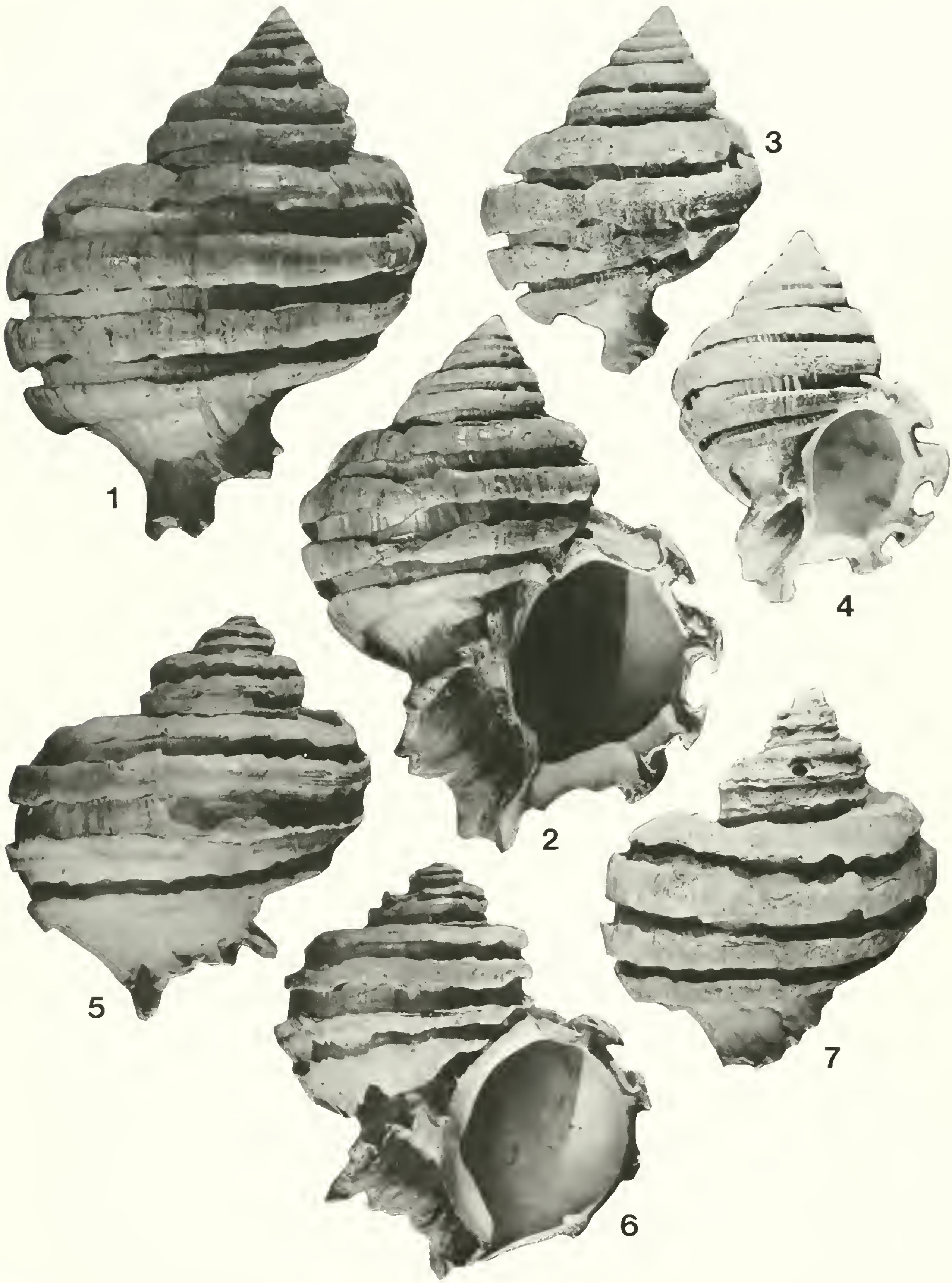
The biogeographic and stratigraphic ranges of *E. parvicostata* are still in debate, as the type locality given by Pilsbry (1911) appears to be in error. The three specimens in Pilsbry's type lot were mixed in with specimens of *E. tricostata* Martin, 1904, and since that species is only known from the Miocene, and mostly from Maryland, Pilsbry assumed that his *E. parvicostata* was also from the Chesapeake Miocene. Since the collector was unknown, no more information about the type locality could be gathered. Subsequent extensive collecting in the Miocene formations of Maryland (Calvert, Choptank, Little Cove Point Unit, and St. Mary's), Virginia (Eastover) (Ward and Blackwelder, 1980), and North Carolina (Pungo River), have failed to uncover any large *Ecphora* species that even remotely resemble *E. parvicostata*.

The finding of three specimens of *E. parvicostata* in the Buckingham Formation at Sarasota documents the species as being Pliocene in age. Dr. Emily Vokes (personal communication) told me of two specimens of *E. parvicostata* in the Tulane University paleontology collections, one from the Yorktown Formation at Rice's Pit and the other from the Jackson Bluff Formation of northern Florida. These two specimens further support a Pliocene age for the species. Wilson (1987) also stated that *E. parvicostata* "must come from Virginia", but considers it "only an extreme variation of *E. quadricostata*". Considering the great differences in the juvenile shells of *E. quadricostata* and *E. parvicostata* and the larger size and more inflated body whorl of the adult *E. parvicostata*, I believe that the two species are distinct, albeit closely related. All three Sarasota specimens of *E. parvicostata* differ from Pilsbry's type in having five ribs instead of four, but are otherwise identical in form.

Ecphora striatula Petuch, 1986
(figure 13)

Ecphora striatula Petuch, 1986:406, pl. 3, figs. 15, 16.

Material examined: Holotype, length 31 mm, Unit 10 of Macasphalt Pit Mine #0800826, Sarasota, Florida, MCZ 29225; paratype (fragment of spire), length 11 mm, "Lakes of the Meadows" subdivision, Bird Road, western Metropolitan Miami, Dade County, Florida, from 20 m depth dredge site, MCZ 29235; length 70 mm, encased in limestone, from boulder along Tamiami Trail near Ochopee, Collier County, Florida, Petuch collection, illustrated here.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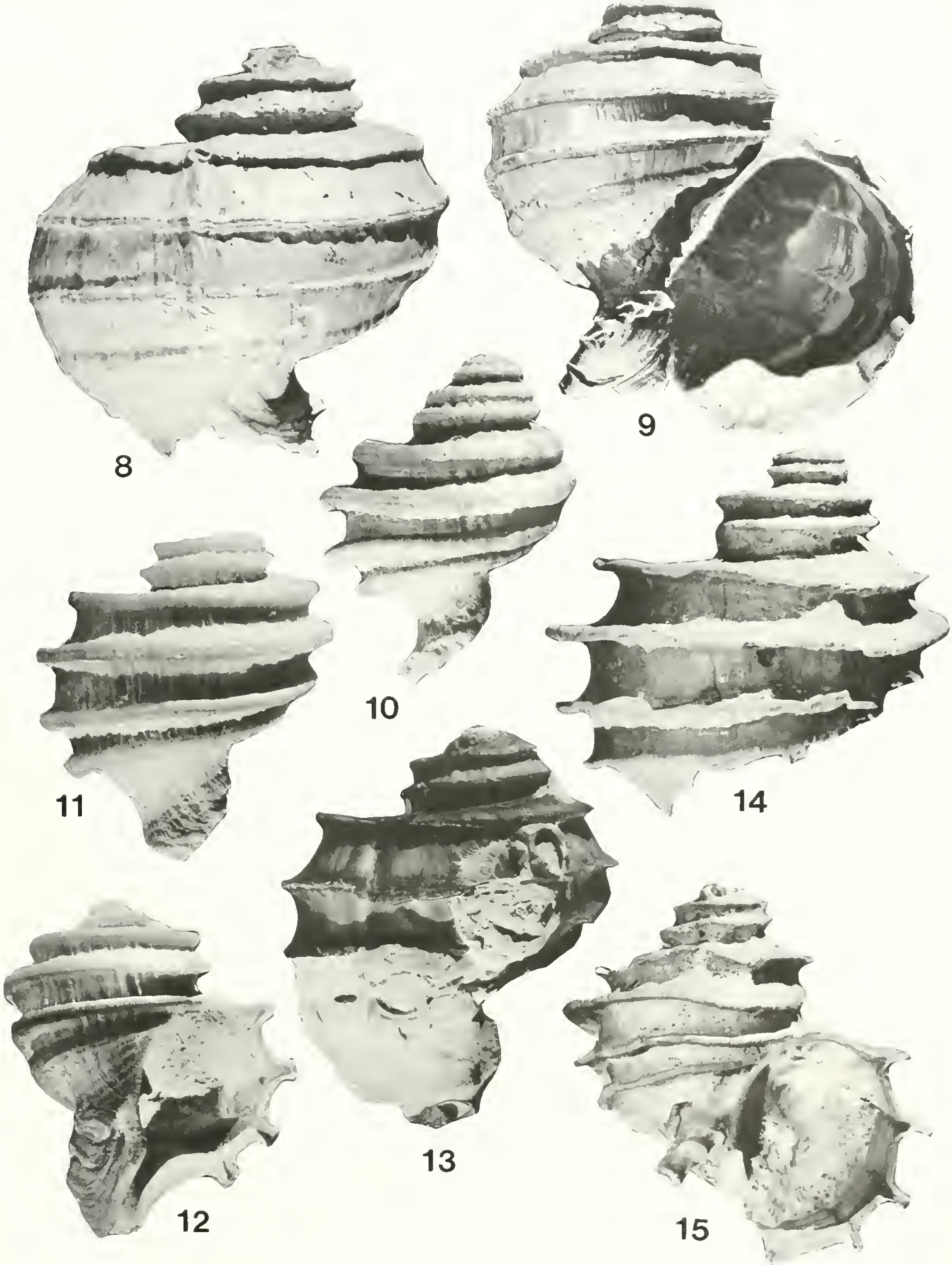

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Discussion: Morphologically, the closest species to *Ecphora striatula* is *E. hertweckorum*. The differences between the two species are discussed under *E. hertweckorum*. Although contemporaneous with *E. hertweckorum*, *E. striatula* appears to have had different ecological preferences, and the two species have not been collected together. At Bird Road in Miami, *E. striatula* (fragmentary paratype) was collected along with massive reef corals and a large fauna of coral reef-associated mollusks (Petuch, 1986). The Tamiami Trail specimen was found encased in a block of reefal limestone, also indicating that *E. striatula* inhabited coral reefs.

The holotype of *E. striatula* from Sarasota, although not found along with massive reef corals, was collected in a dense biohermal assemblage of the interlocking branching coral *Septastraea crassa* (Holmes, 1858) in the Macasphalt Pit. *Ecphora hertweckorum*, on the other hand, appears to have been a lagoonal, soft substrate species, and is usually found together with the large lagoonal bivalves *Chesapecten septenarius* (Say, 1824) and *Carolinapecten eboreus* (Conrad, 1833). *Ecphora striatula* can be considered an index fossil for the fossil reefs and bioherms of the oval-shaped "Everglades Pseudoatoll" (Petuch, 1986, 1987).

Ecphora bradleyae new species
(figures 1–6)

Material examined: HOLOTYPE—length 66 mm, Unit 10 of Macasphalt Newburn Pit Mine #0800826, Sarasota, Florida, USNM 358548; PARATYPES—length 33 mm, same locality as holotype, MCZ 29447; length 76 mm, same locality as holotype, MCZ 29449; fragment, 95 mm, same locality as holotype, MCZ 29450; 3 specimens, lengths 85–105 mm, same locality as holotype, Petuch collection.

Description: Shell turbinate in form, thickened, with 4 wide, flattened spiral ribs on body whorl; ribs strongly "T"-shaped in cross section (figure 20); some specimens with ribs almost touching along edges; ribs ornamented with 4–8 fine, incised grooves; shell smooth and unornamented between and beneath grooves; shoulders rounded; spire elevated, with sloping outline; columella adherent; umbilicus open, flaring; siphonal canal well developed; aperture moderate in size for genus, round in shape; spire whorls with 2 ribs per whorl; suture and edge of shoulder rib separated by wide space, giving spire tabulate appearance; calcitic outer shell layer colored cream-tan or reddish-gray.

Range: Known only from Unit 10 of the Macasphalt Newburn Pit Mine #0800826, Sarasota, Florida. Buckingham Formation, early Pliocene.

Etymology: Named for Mrs. Evelyn Bradley, of Bradenton, Florida, who collected the holotype.

Discussion: *Ecphora bradleyae* differs from the other known members of the genus in having extremely well developed "T"-shaped ribs, and in having a more rounded, fusiform outline. The flanges of the "T"-shaped ribs of some specimens almost coalesce (such as in the paratype shown here in figure 7), in effect producing a double shell. This may have been an anti-crab predation adaptation; doubling the effective shell thickness without doubling the shell weight, and therefore, making it more difficult for peeling crabs, such as *Menippe*, to break back the outer lip. The small paratype (figures 3, 4) has a large healed break that probably resulted from an unsuccessful crab attack.

Ecphora hertweckorum new species
(figures 14, 15)

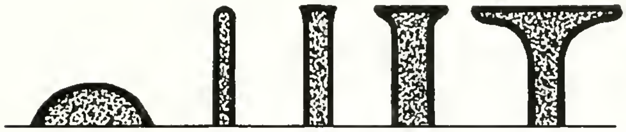
Material examined: HOLOTYPE—length 50 mm (missing siphonal canal), Unit 11, Macasphalt Pit Mine #0800826, Sarasota, Florida, MCZ 29448; PARATYPES—3 fragmentary specimens, lengths 35–47 mm, same locality as holotype, MCZ 29451; length 90 mm (fragmentary), same locality as holotype, Petuch collection.

Description: Shell inflated, thin, delicate; body whorl with 4 very thin, greatly-projecting, bladelike spiral ribs; ribs (figure 17) rounded along edges without "T"-shaped flange; shoulder sharply angled; spire elevated, scalariform; spire whorls with 2 ribs per whorl; shell smooth between ribs, without sculpturing; umbilicus wide, flaring; calcitic outer shell layer colored cream to yellowish-tan.

Range: Known only from Unit 11 in the Macasphalt Newburn Pit Mine #0800826, Sarasota, Florida. Buckingham Formation, early Pliocene. The fragment illustrated by Olsson and Petit, 1964 (as "*Ecphora quadri-*

Figures 1–7. *Ecphora bradleyae* new species, from Unit 10 in the Macasphalt Newburn Pit Mine, Sarasota, Florida. **1, 2.** Holotype, 66 mm, USNM 358548. **3, 4.** Paratype, 33 mm, MCZ 29447. **5, 6.** Paratype, 105 mm, Petuch collection. **7.** Paratype, 76 mm, MCZ 29449

Figures 8–15. **8, 9.** *Ecphora parvicostata* Pilsbry, 1911, 92 mm, Macasphalt Newburn Pit Mine, Unit 11. **10.** *Ecphora quadricostata* (Say, 1824), 30 mm (broken), Macasphalt Newburn Pit Mine, Unit 11. **11, 12.** *Ecphora quadricostata* (Say, 1824), 29 mm, Cape Coral, Lee Co., Florida, MCZ 29453. **13.** *Ecphora striatula* Petuch, 1986, 70 mm (partially covered with limestone and barnacles), along Tamiami Trail near Ochopee, Collier Co., Florida. **14, 15.** *Ecphora hertweckorum* new species, holotype, 50 mm (incomplete), Macasphalt Newburn Pit Mine, Unit 11, MCZ 29448.



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Figures 16–20. Cross sections of the ribs of Floridian *Ecphora* species. **16.** *Ecphora parvicostata* Pilsbry, 1911. **17.** *Ecphora hertweckorum* new species. **18.** *Ecphora striatula* Petuch, 1986. **19.** *Ecphora quadricostata* (Say, 1824). **20.** *Ecphora bradleyae* new species.

costata umbilicata Wagner", pl. 82, fig. 7), from Pinecrest, Collier County, Florida, may be this species.

Etymology: Named for Mr. and Mrs. Charles (and Violet) Hertweck of Venice, Florida, in recognition of their extensive fossil collecting around southern Florida, which has resulted in the discovery of many new species.

Discussion: *Ecphora hertweckorum* is most similar to the contemporaneous *E. striatula* Petuch, 1986 (figure 13). That species, however, differs in being more inflated, ovate, and lower spired, in being heavily sculptured with numerous raised threads between the ribs and on the siphonal canal, and in having flattened edges on the ribs. *Ecphora hertweckorum* is characteristically unornamented with no sculpturing between the ribs or on the siphonal canal, and has rounded edges on the ribs. The spire of *E. hertweckorum* is also more elevated than that of *E. striatula*, and has an obvious stepped appearance.

From the ubiquitous *E. quadricostata* (figures 11, 12), *E. hertweckorum* differs in being a much thinner, much more inflated shell with more prominent, bladelike ribs. Besides being thinner and more fragile, the ribs of *E. hertweckorum* lack the obvious "T"-shaped flanges seen on the ribs of *E. quadricostata*. *Ecphora hertweckorum* is very similar both in shell shape and in the structure of the ribs, to the un-named species from the Miocene Choptank Formation of Maryland that was illustrated by Martin (1904: pl. LII, fig. 4). Although Martin referred the Choptank species to the taxon "*Ecphora quadricostata* var. *umbilicata* (Wagner)", Wilson (1987) has shown that that name is referable to the Pliocene *E. quadricostata*, leaving the Choptank species nameless. The thin-ribbed Choptank species, which Martin described as having ribs that were not "T"-shaped and as being thinner than typical *E. quadricostata* (and presumably *E. gardnerae*), may be the direct ancestor of *E. hertweckorum*. If that is the case, then there may be separate evolutionary lineages for both the thin-ribbed species and those with "T"-shaped ribs.

KEY TO THE FLORIDIAN *ECPHORA* SPECIES

The shape, size, arrangement, and degree of development (projecting from the body whorl) of the ribs on *Ecphora* species are consistent and important taxonomic characters. The rib shape is best seen in cross section (figures 16–20) or in profile at the edge of the aperture. On a few species, secondary sculpturing on the body whorl between the ribs is also an important taxonomic character. See Wilson (1987) for a review of the genus.

1a. Ribs depressed, adherent, cordlike, rounded (figure 16) . . . . *E. parvicostata*
1b. Ribs elevated, projecting from body whorl (figures 17–20) 2
2a. Ribs very thin, bladelike, with rounded edges (figure 17); body whorl smooth . . . *E. hertweckorum*
2b. Ribs very thin, bladelike, with squared edges (figure 18); body whorl sculptured with spiral threads . . . . *E. striatula*
2c. Ribs with laterally-expanded terminal flanges (figures 19, 20) 3
3a. Ribs with slightly-developed terminal flanges; slightly "T"-shaped in cross section (figure 19) . . . . *E. quadricostata*
3b. Ribs with greatly-developed, broad terminal flanges; distinctly "T"-shaped in cross section (figure 20) . . . . *E. bradleyae*

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LITERATURE CITED

Conrad, T. A. 1830. On the geology and organic remains of a part of the peninsula of Maryland; with appendix. Journal of the Academy of Natural Sciences of Philadelphia 6:205–230, pls. 9, 10.

Conrad, T. A. 1843. Descriptions of a new genus, and of twenty-nine new Miocene, and one Eocene fossil shells of the United States. Proceedings of the Academy of Natural Sciences of Philadelphia 1:305–311.

Hazel, J. F. 1983. Age and correlation of the Yorktown (Pliocene) and Croatan (Pliocene and Pleistocene) formations at the Lee Creek Mine. *In:* Ray, C. (ed.). Geology and paleontology of the Lee Creek Mine, North Carolina, I. Smithsonian Contributions to Paleobiology 53:81–122, 38 pls.

Mansfield, W. C. 1930. Miocene gastropods and scaphopods of the Choctawhatchee Formation of Florida. Florida State Geological Survey, Bulletin 3:1–190, 21 pls.

Mansfield, W. C. 1939. Notes on the Upper Tertiary and

Pleistocene Mollusks of Peninsular Florida. State of Florida Department of Conservation, Geological Bulletin 18:7–16, table 1

Martin, G. C. 1904 Systematic paleontology: Gastropoda Maryland Geological Survey, Miocene, p 131–270, pls. 39–63

Olsson, A. A. 1968 A review of the Late Cenozoic stratigraphy of southern Florida. *In:* Perkins, R D (ed.). Late Cenozoic stratigraphy of southern Florida—a reappraisal. Miami Geological Society, p. 66–82, 2 pls.

Olsson, A. A and R E. Petit. 1964. Some Neogene Mollusca from Florida and the Carolinas. Bulletins of American Paleontology 47(217):509–575, pls. 77–83.

Petuch, E. J. 1982. Notes on the Molluscan paleoecology of the Pinecrest Beds at Sarasota, Florida with the description of *Pyruella*, a stratigraphically important new genus (Gastropoda: Melongenidae). Proceedings of the Academy of Natural Sciences of Philadelphia 134 12–30, 3 figs., 3 pls.

Petuch, E. J. 1986. The Pliocene reefs of Miami: their geomorphological significance in the evolution of the Atlantic Coastal Ridge, southeastern Florida, U.S.A. Journal of Coastal Research 2(4):391–408, 5 figs., 4 pls.

Petuch, E. J 1987. The Florida Everglades: a buried pseudoatoll? Journal of Coastal Research 3(2):189–200, 9 figs.

Pilsbry, H. A 1911. A new *Ecphora* of the Chesapeake Miocene. Proceedings of the Academy of Natural Sciences of Philadelphia (May):438–439, fig. 1.

Say, T 1824 An account of some of the fossil shells of Maryland. Journal of the Academy of Natural Sciences of Philadelphia 4.124–155, pls. 7–13.

Tuomey, M. and F. S. Holmes. 1857. Pleiocene fossils of South-Carolina. James and Williams, Printers, Charleston, p. i–xvi, 1–152, 30 pls.

Ward, L. W. and B W. Blackwelder. 1980. Stratigraphic revision of Upper Miocene and Lower Pliocene beds of the Chesapeake group, Middle Atlantic Coastal Plain. U.S. Geological Survey Bulletin 1482-D (Contributions to Stratigraphy), 61 p., 25 figs., 5 pls.

Wilson, D. 1987. Species of *Ecphora*, including the subgenus *Stenomphalus*, in the Pungo River Formation. *In:* Ray, C. (ed.). Geology and paleontology of the Lee Creek Mine, North Carolina, II. Smithsonian Contributions to Paleobiology 61:21–29, 1 fig., 2 pls.

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